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THÈSE

Pour obtenir le grade de
Docteur

Délivré par
UNIVERSITE MONTPELLIER II – SCIENCES ET TECHNIQUES

Préparée au sein de l'école doctorale SIBAGHE
Et de l'unité de recherche CNRS, UMR 5175

Spécialité : **Écologie, Évolution, Ressources
Génétiques, Paléontologie**

Présentée par **Soizic LE SAOUT**

**Comprendre les fortes densités de cerfs en
milieux fortement abrutis : le rôle de la
nourriture et de la peur chez le cerf à-
queue-noire de Sitka**

Soutenue le Mardi 03 Décembre 2013 devant le jury composé de

Mr. Jean-Louis MARTIN, Directeur de Recherches, CEFE- CNRS, Montpellier	Co-Directeur de Thèse
Mr. Simon CHAMAILLE-JAMMES, Chargé de Recherches, CEFE-CNRS, Montpellier	Co-Directeur de Thèse
Mr. Daniel BLUMSTEIN, Professeur et Directeur de Recherches, University of California, Los Angeles	Rapporteur
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Mme Anne CHARMANTIER, Chargée de Recherches, CEFE- CNRS, Montpellier	Examinatrice
Mme. Sonie SAÏD, Chargée d'Etudes et de Recherches, ONCFS-DER, CNERA Cervidés Sanglier, Birieux	Examinatrice

UNIVERSITE MONTPELLIER II – SCIENCES ET TECHNIQUES

THESE

Pour obtenir le grade de
DOCTEUR DE L'UNIVERSITE MONTPELLIER II

Discipline : Biologie de l'Evolution et Ecologie
Spécialité : Écologie, Évolution, Ressources Génétiques, Paléontologie
Ecole doctorale : Systèmes Intégrés en Biologie, Agronomie, Géosciences,
Hydrosciences, Environnement (SIBAGHE)

Par
Soizic LE SAOUT

**Comprendre les fortes densités de cerfs en milieux fortement abrutis: le rôle de la nourriture
et de la peur chez le cerf à-queue-noire de Sitka**

**Understanding high densities of deer in a heavily browsed habitat: a study on food and fear in
Sitka black-tailed deer**

Co-Directeur : Dr. Jean-Louis MARTIN (CEFE-CNRS, Montpellier)

Co-Directeur : Dr. Simon CHAMAILLE-JAMMES (CEFE-CNRS, Montpellier)

Soutenance: Mardi 03 Décembre 2013

Membres du jury

Daniel BLUMSTEIN, Professeur et Directeur de Recherches, University of California, Los Angeles	Rapporteur
Hervé FRITZ, Directeur de Recherches, LBBE-CNRS, Lyon	Rapporteur
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Laboratoire d'accueil :

Centre d'Ecologie Fonctionnelle et Evolutive, 1919 Route de Mende, 34090 Montpellier, France

TITRE :

Comprendre les fortes densités de cerfs en milieux fortement abrutis : le rôle de la nourriture et de la peur chez le cerf à-queue-noire de Sitka

Mots-clés :

Ecologie de la peur, Grands Herbivores, Risques de prédation, Ajustements comportementaux et physiologiques, Surabondance.

RESUME COURT :

Les fortes densités actuelles de cerfs causent des problèmes écologiques et socio-économiques. Ces densités restent élevées malgré la forte dégradation des milieux qu'elles occasionnent. Nous explorons les mécanismes qui expliquent ce paradoxe en étudiant les compromis entre disponibilité en ressources et réponses au risque de prédation dans des situations contrastées de nourriture et de risque sur trois îles de Haïda Gwaii (Canada). Les chutes de feuilles de la canopée et la pousse annuelle de plantes rhizomateuses aident au maintien de fortes densités de cerfs. Malgré l'absence de prédation les cerfs maintiennent des comportements de vigilance, réagissent négativement à l'urine de loup, et semblent gérer le risque spatialement plutôt qu'en étant vigilants. Exposés à une chasse expérimentale de basse intensité seuls les cerfs les moins tolérants à la perturbation humaine évitent la zone chassée. Nous discutons les implications de ces résultats pour gérer les populations de cerfs.

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RESUME LONG :

L'augmentation de populations de cerfs pose d'importants problèmes écologiques et socio-économiques à l'échelle locale et mondiale. Des signes de densité-dépendance sont souvent observés, mais les cerfs restent abondants malgré l'importante dégradation du milieu qu'ils provoquent. Ceci soulève la question de l'ajustement des cerfs aux changements de milieu qu'ils créent ? Nous avons abordé cette question en recherchant comment les cerfs gèrent leur ressource alimentaire en fonction du risque de prédation. La prédation, en plus de son effet létal (élimination de proie), peut moduler le comportement et la physiologie des proies (effet non-létal) qui doivent balancer le fait de se nourrir et le risque de prédation. Cette étude contribue à mieux comprendre comment les cerfs maintiennent d'abondantes populations dans des milieux qu'ils ont eux-mêmes appauvris.

Notre projet s'est intéressé au cerf à-queue-noire Sitka (*Odocoileus hemionus sitkensis*) sur trois îles de l'archipel de Haïda Gwaii (BC, Canada). Ces îles sont dépourvues des principaux prédateurs naturels du cerf (loup et puma) et ont été colonisées par les cerfs il y a plus de 60 ans. Lors de notre étude, ces îles présentaient des niveaux contrastés de nourriture et de risque de prédation : sur deux îles, les cerfs vivaient sans prédateur mais avaient fortement appauvri leur milieu (îles sans risque/pauvres). Sur la troisième île, les cerfs étaient chassés et bénéficiaient d'un sous-bois forestier partiellement restauré comme nourriture (île risquée/riche).

Dans ce cadre, nous avons étudié : 1) quelles sont les ressources qui permettent aux cerfs de maintenir des populations denses dans des milieux très abrutis ?; 2) comment le stress alimentaire ou le risque de prédation influencent-ils la réponse physiologique des cerfs au stress?; 3) des cerfs naïfs à la prédation conservent-ils des niveaux de vigilance dans des milieux très abrutis et répondent-ils à des stimuli olfactifs de prédateurs ?; et 4) comment, dans des milieux très abrutis, des cerfs naïfs à la prédation répondent-ils à une chasse expérimentale pour faire peur et comment cela affecte-t-il la végétation ?

Notre étude a montré que : 1) les chutes de feuilles de la canopée et la pousse annuelle de plantes rhizomateuses offraient une grande quantité d'énergie pour les cerfs et contribuaient

au maintien de denses populations de cerfs dans des milieux appauvris ; 2) La présence de stress alimentaire ou de risque de prédation n'affectaient pas la réponse physiologique des cerfs au stress, suggérant l'existence d'ajustements comportementaux et/ou physiologiques permettant de réduire l'exposition des cerfs à ces deux facteurs de stress ; 3) sur les îles sans risque/pauvres, les cerfs ont maintenu la vigilance malgré 60 ans d'isolation à la prédation. En outre, les cerfs naïfs à la prédation évitaient de manger en présence d'urine de loup (dangereux) mais pas en présence d'urine d'ours (moins dangereux), suggérant que les cerfs présentaient une stratégie innée de nourrissage sensible au risque. Les cerfs restaient aussi moins longtemps aux stations d'appâts en présence d'urine de loup mais n'augmentaient pas leur niveau de vigilance, suggérant qu'ils géraient le risque spatialement plutôt que par la vigilance ; 4) En réponse à une chasse expérimentale pour faire peur, réalisée sur une des îles sans risque/pauvres, seuls les cerfs les moins tolérant à la perturbation humaines évitaient la zone chassée. Ceci souligna l'importance de la sélection des traits comportementaux induite par l'homme dans la gestion de la faune et de la flore. Nous avons aussi suivi la croissance de quatre espèces de plantes côtières à croissance rapide et avons montré que notre chasse expérimentale favorisait la croissance de la moitié d'entre elles, soulignant l'interaction complexe entre le comportement de nourrissage et les caractéristiques des plantes, ainsi que l'importance des objectifs dans le choix des outils de gestion.

TITLE:

Understanding high densities of deer in a heavily browsed habitat: a study on food and fear in Sitka black-tailed deer

Key-words:

Fear ecology, Large herbivores, Predation risks, Behavioral and physiological adjustments, Overabundance

BRIEF ABSTRACT:

In many places deer population have increased in abundance raising serious ecological and socio-economic concerns. Despite the severe degradation deer cause on their own environment, deer seem to remain abundant. How do they do? Predation may have severe impacts on deer behavior and physiology because deer have to trade safety for food. We studied how deer manage food resource and predation risk on three islands of Haida Gwaii (Canada) with contrasted levels of food and risk. We showed that canopy litterfall and the growth of perennial rhizomatous plants help supporting dense deer populations. Predator-naïve deer maintained anti-predation behaviors like vigilance, responded negatively to wolf urine and were likely to manage risk more by space than by vigilance. In response to an experimental low-intensity hunting only the deer the less-tolerant to human disturbance avoided the hunting area. We discussed the long-term effects of hunting as management tool for abundant deer populations.

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LONG ABSTRACT:

In many temperate environments deer populations have been increasing, raising serious ecological and socio-economic concerns both locally and globally. Signs of density dependence are often observed in such populations, but deer abundance often remains high with regard to the dramatic degradation of the environment they have induced. This raises the question: How do deer do to adjust to the environmental changes they created? The present study addressed aspects of this question focusing on how deer manage their food resource in relation to predation risk. In addition to its consumptive effect (prey removal), predation is increasingly recognized for its non-consumptive effect on prey behavior and physiology, the importance of which is linked to the strength of the trade-off between foraging and predation risk. A better understanding on how deer manage food resource and predation risk in heavily browsed environment may thus help to better understand how deer maintain abundant populations in self-induced depleted environment.

We tackled this question by studying Sitka black tailed deer (*Odocoileus hemionus sitkensis*) on three islands of the Haida Gwaii archipelago (B.C., Canada). These islands are devoid of the main natural predators of deer (wolves and cougars) and were colonized by deer over 60 years ago. At the time of the study, these islands presented contrasted levels of food and predation risk: on two islands, deer were predator-free but had strongly depleted their environment (safe/poor islands). On the third island, deer were culled by means of regular hunts and had access to a partially recovered forest understory in terms of food supply (risky/rich island).

We considered four questions: 1) on what resources do abundant deer populations rely in heavily browsed environment?; 2) how do deer physiological stress response vary with either food stress or predation risk?; 3) do predator-naïve deer maintain anti-predator behaviors, like vigilance, in heavily browsed environments and how do they respond to predator olfactory cues?; and 4) how do predator-naïve deer respond to an experimental hunting for fear in a heavily browsed environment and how does it affect the vegetation?

We showed that: 1) the subsidies from canopy litterfall and the annual growth from rhizomatous plants offered a large energy supply for deer and contributed to maintain abundant deer population in forests with depleted understory; 2) deer did not mount a physiological stress response in presence of either starvation or predation risks, and we suggested that behavioral and/or physiological adjustments allowed deer to mitigate their

exposure to either stressor; 3) on safe/poor islands, deer maintained vigilance despite 60 years of isolation from predation. Predator-naïve deer avoided eating bait in presence of urine of wolf (dangerous) but not of bear (less dangerous). This suggested an innate threat-sensitive foraging strategy in deer. Deer also remained less time at the bait stations in presence of wolf urine but did not increase their vigilance levels. This suggested that deer were likely to manage risk more by space use than by vigilance; 4) In response to an experimental hunting for fear conducted on one of the safe/poor island, we showed that the deer less-tolerant to humans avoided the hunting area; The deer more-tolerant to human disturbance did not. This stressed the importance to consider the human-induced selection of behavioral traits during wildlife management. We also monitored the growth of four fast-growing coastal plant species and showed that the hunting for fear promoted the growth of half of them. This highlighted the intricate interaction among deer foraging behavior and plant characteristics and emphasized the importance of management targets in the choice of management tools. We discussed the long-terms effect of hunting as management tool for deer.

RESUME SUBSTANTIEL – FRENCH PROCEEDINGS

Contexte & Problématique : Surabondance de cerfs ; le rôle de la nourriture et de la prédation

Dans un contexte mondial de perte de diversité biologique, il est étonnant de noter que localement des espèces de grands herbivores, tels que les cerfs (genres : *Cervidae*, *Moschidae* et *Tragulidae*), ont vu leurs populations croître au point d'être parfois qualifiées de « surabondantes » (McShea et al. 1997). La surabondance, d'un point de vue écologique, peut se définir par l'existence de populations qui, de par leur abondance, menacent le fonctionnement des écosystèmes (Caughley 1981). Sous cette définition des populations de cerfs ont été qualifiées de surabondantes dans la majorité des milieux tempérés dans le monde (ex : Europe, continent Nord-Américain, Japon, Nouvelle Zélande : revue dans Chollet 2012, Tableau 12). Localement, l'émergence de ces abondantes populations de cerfs peut s'expliquer par de nombreux facteurs, tels que la modification de l'utilisation des sols, créant des habitats favorables pour les cerfs (ex. mélange d'espaces boisés et céréaliers), le nourrissage hivernal, l'élimination des grands carnivores ou encore les quotas de chasses favorisant la survie des femelles et des faons (revue dans Côté et al. 2004 ; Tanentzap et al. 2012). Sous ces conditions des populations de cerfs ont vu leurs abondances croître localement, causant d'importants problèmes écologiques et socio-économiques (revue dans Mcshea et al. 1997 ; Côté et al. 2004). Parmi ces derniers, on peut citer, la perte de biodiversité des milieux forestiers (ex. diminution de l'abondance et de la diversité des communautés de plantes, d'oiseaux et d'insectes), la modification des cycles géochimiques (ex. cycle du carbone et de l'azote), la réduction des rendements des activités sylvo-agricoles, l'augmentation des accidents de la route liés à des collisions cerf-véhicule, ou encore l'augmentation du risque de zoonose (ex. maladie de Lyme).

Face à ces enjeux, une meilleure compréhension de la relation entre le cerf et son milieu semble primordiale. Ceci semble d'autant plus critique que ces fortes populations de cerfs, en dégradant leur milieu, dégradent également leur propre ressource alimentaire. Et pourtant les cerfs semblent capables de maintenir de fortes densités. Comment font-ils ? Cette étude s'intéresse à cette problématique et se concentre sur le rôle des ressources alimentaires et du risque de prédation dans le maintien de fortes densités de cerfs. En effet, d'un côté les

ressources alimentaires peuvent limiter la survie et/ou la reproduction des cerfs lorsqu'elles sont en quantité insuffisante et/ou de trop faibles qualités nutritionnelles (revue Parker 2003, 2009). Ceci est à la base du concept de densité-dépendance, selon lequel l'augmentation de la densité d'une population est corrélée à la raréfaction des ressources de cette même population, limitant alors la croissance de cette population. Ce mécanisme est particulièrement important dans la dynamique des populations de grands herbivores comme les cerfs (revue dans Bonenfant et al. 2009) et accentue la nécessité de mieux comprendre comment les cerfs dans des milieux fortement abrutis s'ajustent à l'appauvrissement de leurs ressources, appauvrissement qu'ils ont créé eux-mêmes. D'un autre côté la prédation peut également limiter la survie et/ou la reproduction des cerfs par son effet létal (élimination d'individus proies) et ses effets non-létaux (modifications comportementales et/ou physiologiques des cerfs liées au risque de prédation) (Lima 1998a, 1998b). Les effets non-létaux de la prédation peuvent se comprendre comme les coûts liés à l'investissement de temps, d'énergie et/ou de nutriments dans la mise en place de comportements anti-prédateurs et/ou d'une réponse physiologique à la présence du risque de prédation, au détriment d'autres activités telles que la reproduction ou la subsistance.

D'un point de vue comportemental ces coûts peuvent s'interpréter à la lumière du compromis entre le niveau de risque, le niveau de gain et l'état de l'individu proie (état physiologique et nutritionnel) (Lima & Dill 1990). Toutes choses égales par ailleurs, la théorie prédit que : i) en réponse à une diminution du risque, un individu proie devrait investir moins de temps et/ou d'énergie dans des comportements anti-prédateurs car les gains associés en terme de valeur sélective (future reproduction si l'individu survit) diminuent puisque le risque d'être tué diminue ; ii) en réponse à une augmentation du gain, un individu proie devrait investir moins de temps et/ou d'énergie dans des comportements anti-prédateurs car les gains associés en terme de valeur sélective diminuent du fait d'une augmentation des coûts liés aux opportunités manquées telle que l'opportunité de se nourrir; et iii) en réponse à une diminution de son état, un individu proie devrait investir moins de temps et/ou d'énergie dans des comportements anti-prédateurs si les gains associés en terme de valeur sélective diminuent : i.e. un animal affamé, ayant une plus faible probabilité de se reproduire dans le futur, a moins de gains en investissant

dans des comportements anti-prédateurs qu'un animal en bonne santé ayant une plus forte probabilité de se reproduire s'il survit au risque de prédation. Cette évaluation du risque, du gain et de l'état de l'individu proie aboutit à une prise de décision par l'individu proie qui dépend de sa propre perception de ces trois constituants. L'acquisition et le traitement de l'information acquise d'une part, l'expérience passée d'une proie et ses caractéristiques héritées (ex. comportement inné) d'autre part, interagissent donc dans la prise de décision de l'individu proie pour gérer le risque de prédation (Lima 1998a, 1998b ; Blumstein & Bouskila 1996 ; Lima & Steury 2005 ; Relyea 2005). De nombreuses stratégies anti-prédatrices existent (revue dans Caro 2005), parmi lesquelles la gestion de l'espace (ex. sélection des habitats et évitement des zones risquées) et du temps [ex. temps passé en vigilance (conscience visuelle de l'environnement permettant une détection précoce des prédateurs)] sont des éléments clés du comportement anti-prédateur chez les cerfs (ex. Lung & Childress 2007 ; Bonnot et al. 2013).

La réalisation que le risque de prédation pouvait modifier l'utilisation spatio-temporel du milieu par des individus proies et de ce fait que le risque de prédation pouvait modifier les interactions entre les individus proies et leur milieu, a ouvert une nouvelle avenue de recherche, popularisée sous le terme d' « écologie de la peur ». Cette discipline examine comment le risque de prédation influence la structure et le fonctionnement des écosystèmes. Elle fut particulièrement soutenue par la célèbre histoire du Parc National du Yellowstone, Wyoming, E.U., où, depuis le retour du loup (*Canis lupus*), les cerfs élaphe (*Cervus elaphus*), considérés comme surabondants dans le parc, sont devenus plus vigilants et ont évité certains milieux permettant la régénération de plantes fortement broutées tel que le peuplier faux-tremble (*Populus tremuloides*) (Laundré et al. 2001 ; Creel et al. 2005). Toutefois, les mécanismes fins à l'origine de ces changements à l'échelle de l'écosystème sont encore débattus, et en particulier l'importance relative de l'effet létal et des effets non-létaux de la prédation sur la dynamique observée ne semblent pas encore résolus (Middleton et al. 2013). Cet exemple met en évidence une question au cœur des recherches actuelles sur les modes de gestion des fortes densités de cerfs dont l'un des objectifs est de savoir si les risques de prédation, par eux seuls, peuvent réduire les effets négatifs des cerfs sur leur milieu et si la gestion anthropique de ce risque de prédation peut permettre de gérer les surabondances de cerfs.

D'un point de vue physiologique, un individu répond à la présence d'un facteur de stress (i.e. élément perturbant l'homéostasie, l'équilibre physiologique interne, d'un individu) en montant une cascade physiologique, nommée « réponse au stress ». Cette cascade permet de neutraliser les effets délétères d'une homéostasie perturbée par des ajustements physiologiques et/ou comportementaux (ex. fuite devant un danger) (Reeder & Kramer 2005 ; Wingfield 2003). Cette réponse au stress est coûteuse à mettre en place et à maintenir et implique une réallocation des ressources (énergie et/ou nutriments) entre les activités de reproduction, de croissance et de maintenance. Cette cascade physiologique est orchestrée par diverses neuro-hormones et hormones telles que les glucocorticoïdes, des hormones stéroïdiennes, qui voient leur concentration plasmatique augmentée en présence d'un facteur de stress. Les glucocorticoïdes contribuent à court et à moyen termes à mobiliser et à allouer l'énergie nécessaire pour faire face au facteur de stress et restaurer l'homéostasie de l'individu au détriment de la reproduction, de la croissance et du système immunitaire. Si cette réallocation d'énergie est maintenue sur le long-terme elle peut avoir des conséquences délétères sur la survie et la reproduction de l'individu. Le maintien de forts niveaux de glucocorticoïdes, causés par une exposition prolongée et/ou répétitive à un facteur de stress, est appelé « stress chronique » (revue dans Sapolsky et al. 2000 ; McEwen & Wingfield 2003; Romero 2004 ; Reeder & Kramer 2005). Par exemple, Boonstra et al. (1998) ont montré que les lièvres d'Amérique (*Lepus americanus*) exposés à des années successives de fortes pressions de prédation présentaient des niveaux basaux de glucocorticoïdes plus élevés, perdaient plus de masses corporelles en hiver, avaient des tailles de portée plus petites et présentaient des niveaux plus élevés d'immunosuppression.

Bien que les effets non-létaux de la prédation soient de plus en plus reconnus, leur conséquences sur la survie et la reproduction des individus proies et leurs effets sur la dynamique de la population des proies sont rarement explicitement établis (revue dans Clinchy et al. 2013) et présentent encore de nombreux défis (ex. Middleton et al. 2013). Ceci d'autant plus, que le risque de prédation peut interagir avec la qualité et la disponibilité des ressources alimentaires et que tous les deux peuvent également interagir avec les conditions environnementales (ex. rudesse du climat, saisons : Mao et al. 2005). Une meilleure

compréhension du rôle de la nourriture et du risque de prédation semble donc importante pour mieux cerner les facteurs limitant ou favorisant le maintien de fortes densités de cerfs localement. Nous abordons cette problématique en répondant à quatre questions : 1) quelles sont les ressources qui permettent aux cerfs de maintenir des populations denses dans des milieux très abrutis?; 2) comment le stress alimentaire ou le risque de prédation influencent-ils la réponse physiologique des cerfs au stress?; 3) des cerfs naïfs à la prédation conservent-ils des niveaux de vigilance dans des milieux très abrutis et répondent-ils à des stimuli olfactifs de prédateurs ?; et 4) comment, dans des milieux très abrutis, des cerfs naïfs à la prédation répondent-ils à une chasse expérimentale destinée à instiller la peur et comment cela affecte-t-il la végétation?

Système d'étude

Pour ce faire nous avons étudié le cerf à queue-noire de Sitka (*Odocoileus hemionus sitkensis*) sur l'archipel de Haïda Gwaii (Colombie Britannique, NO Canada) dépourvu des principaux prédateurs naturels du cerf [loup, puma (*Puma concolor*)], mais sur lequel vit l'ours noir (*Ursus americanus*), un prédateur opportuniste de faons. Le cerf à queue-noire a été introduit sur l'archipel entre 1878 et 1925 en tant qu'espèce gibier et a colonisé il y a plus de 60 ans les trois îles où se situe notre étude, East Limestone Island (ci-après East Limestone), Kunga Island (ci-après Kunga) et Reef Island (ci-après Reef). Ces trois îles sont inhabitées et, en l'absence de prédation (naturelle et chasse), les populations locales de cerfs ont crû et fortement dégradé leur milieu. En particulier, sur ces îles le couvert du sous-bois forestier a été réduit de plus de 90% par rapport au sous-bois forestier sur des îles sans cerfs (revues dans Martin et al. 2010 ; Chollet 2012). Ces changements dans la composition et la structure du sous-bois forestier ont entraîné une réduction de la diversité et de l'abondance des espèces d'insectes et d'oiseaux dépendantes du sous-bois forestier (revue dans Martin et al. 2010 ; Chollet 2012). Face à ce constat, un programme de contrôle de la population de cerfs a été initié en 1997 sur Reef, et a réduit de plus de 70% la densité locale de cerfs dans les trois années suivant la première chasse (Gaston et al. 2008 ; Chollet 2012). L'effort de chasse a été maintenu plus ou moins assidûment depuis et a permis la régénération, au moins partielle, du sous-bois forestier. Aucune chasse n'eut lieu sur East Limestone et Kunga qui présentent au moment de l'étude des forêts dénuées de sous-bois, et dépourvues de la plus part des espèces de plantes traditionnellement identifiées dans le régime alimentaire du cerf à queue-noire (McTaggart Cowan 1956 ; Pojar et al. 1980). Les trois îles de l'étude présentent donc des niveaux de ressources

alimentaires et des niveaux de risques de prédatons contrastés : sur East Limestone et Kunga les cerfs sont naïfs à la prédation mais ont accès à un sous-bois appauvris (îles sans risque/pauvres), alors que sur Reef les cerfs sont chassés mais ont accès à un riche sous-bois (île risquée/riche).

Les activités humaines sur ces trois îles se limitent aux activités de recherches et aux visites occasionnelles de touristes entre mai et août. En outre, East Limestone héberge également de mai à juillet des groupes de volontaires (3-6 individus) impliqués dans les activités de Laskeek Bay Conservation Society, une société de conservation de la nature qui réalise un suivi à long-terme de la faune et de la flore locales. Pendant la période de l'étude (mars 2011 – octobre 2012), aucune chasse n'eut lieu sur Reef, mais des activités de recherche avaient lieu sur l'île et nous supposons que les cerfs de Reef, qui ont été chassés jusqu'en 2010, perçoivent les humains comme de potentiels prédateurs (Frid & Dill 2002).

Afin de pouvoir identifier les cerfs individuellement nous avons conduit trois sessions de capture sur chaque île entre mars-avril 2011 et août-octobre 2012. Nous avons principalement utilisé des boîtes de captures appâtées avec des pommes et des granulés pour capturer les cerfs. Au total nous avons capturé et marqué 24 cerfs sur East Limestone, 22 cerfs sur Kunga et sept cerfs sur Reef.

Chapitre I : Comprendre le paradoxe des cerfs persistant à de forte abondance dans des habitats fortement broutés.

Pour mieux comprendre comment les cerfs pouvaient maintenir de fortes densités dans des milieux très abrutis nous avons réalisé un bilan énergétique comparant l'énergie disponible et l'énergie nécessaire au maintien des populations locales de cerfs sur les trois îles de l'étude. Pour ce faire, nous avons estimé sur le terrain la biomasse annuelle sèche accessible pour les cerfs et produite par trois sources de nourriture : i) le sous-bois ; ii) les flux de sous-bois (pousse annuelle de plantes rhizomateuses cachées dans la mousse et pousse de nouveaux individus issus de la banque de graine) ; et iii) les subventions de la canopée (chute de feuille). Nous avons ensuite considéré deux saisons (été : avril à septembre ; hivers : octobre à mars) et en utilisant des données publiées pour chaque espèce de plantes, nous avons pu estimer pour chaque saison la quantité d'énergie procurée par chacune des trois sources de nourriture. Nous avons comparé ces niveaux d'énergie à ceux estimés pour le maintien sans ou avec reproduction des

populations locales de cerfs. Les coûts métaboliques ont été estimés à partir d'équations publiées dans la littérature et calibrées par le sexe ratio, les âge-ratios (faons : < 10 mois ; sous-adultes : 10-27 mois ; adultes : > 27 mois), la masse corporelle saisonnière moyenne pour chaque sexe et classe d'âge, et la densité locale de cerfs. Ces quatre derniers paramètres ont été estimés sur le terrain lors de captures de cerfs (masse corporelle) et lors d'une session de piège photographique (sexe et âge ratios, densité). En particulier, nous avons pu estimer les densités locales de cerfs grâce à une méthode récente de Capture-Marquage-Recapture qui prend en compte à la fois les animaux marqués, individuellement reconnaissables sur les photographies, et les animaux non-marqués, non-identifiables sur les photographies (Chandler & Royle 2013). Compte tenu de l'incertitude dans les paramètres estimés, et particulièrement dans l'estimation de la biomasse sèche, des masses corporelles et de la densité locale de cerfs, nous avons testé la robustesse de nos résultats en simulant différents jeux de valeurs numériques tirés dans des lois normales centrées sur les valeurs estimées sur le terrain pour ces trois types de paramètres. Nous avons ensuite étudié les bilans énergétiques obtenus. Les simulations présentaient des résultats cohérents avec ceux obtenus avec les valeurs de paramètres mesurés sur le terrain et garantissent la validité des résultats suivants : sur East Limestone et Kunga, les deux îles sans risque/pauvres, les cerfs souffraient d'un déficit énergétique en hiver mais l'énergie disponible en été excédait leurs besoins saisonniers et permettait de maintenir un bilan positif à l'échelle de l'année. Les flux de croissance dans le sous-bois forestiers et les chutes de feuilles représentaient l'essentiel de l'énergie disponible et permettaient le maintien de population reproductrice de cerfs. Ces deux ressources sont rarement considérées comme ressources alimentaires et pourtant elles semblent jouer un rôle capital dans le maintien des fortes densités de cerf actuelles sur les deux îles sans risque/pauvres de l'étude. Étant donné que les flux de sous-bois sont surtout issus de plantes pérennes, tolérantes à l'abrutissement et faiblement impactée par les pressions d'herbivorie, et que la consommation des feuilles au sol n'affecte pas les plantes-mères, la consommation de ces deux types de ressource n'affecte que faiblement ou indirectement la production de ces ressources à court-termes. Des changements dans la structure et la composition du sol peuvent affecter le recrutement, la productivité et/ou la fertilité des plantes-mères et donc la production

de ces ressources mais ceci n'arrivera qu'à long terme. Ce découplage entre consommation et production nous interroge sur l'échelle temporelle à laquelle auront lieu, si elles ont lieu, les boucles de rétroaction négatives attendues entre consommation et production de ressources, boucles qui sont à la base des mécanismes de densité-dépendance. Ce découplage questionne sur l'efficacité du « laisser-faire » comme stratégie de gestion de fortes densités de cerfs en milieux tempérés. Sur Reef, l'île risquée/riche, le bilan énergétique des cerfs était positif toute l'année et le sous-bois forestier, à lui seul, procurait plus de sept fois les niveaux d'énergie nécessaire pour maintenir la population reproductrice actuellement présente sur l'île.

Chapitre II : Faible disponibilité alimentaire ou risque de prédation : quel est le plus stressant pour des cerfs à queue-noire insulaires ?

Pour comparer comment les cerfs répondent physiologiquement à du stress alimentaire ou au risque de prédation, nous avons étudié les niveaux des métabolites glucocorticoïdes fécaux (fecal glucocorticoid metabolites : FGM), un indicateur de stress physiologique chez les animaux, dans 205 échantillons prélevés sur les trois îles entre avril 2011 et mars 2012. Nous prédisions que : i) les niveaux de FGM devraient augmenter en mars, quand la nourriture est plus rare, et en avril quand les cerfs doivent reconstruire leur réserve de graisse et que les femelles sont gravides. Ceci était particulièrement attendu sur les deux îles sans risque/pauvres (East Limestone et Kunga), où les cerfs souffrent d'un déficit énergétique en hiver ; ii) les niveaux de FGM devraient augmenter en présence d'activités humaines potentiellement perturbatrices, et ceci d'autant plus sur l'île risquée/riche (Reef) où les hommes devraient être perçus comme des prédateurs par les cerfs chassés. Nous avons également suivi les variations saisonnières dans la qualité du régime alimentaire des cerfs, en mesurant la teneur en azote des échantillons fécaux. Etant donné que les cerfs étudiés mangent des algues (algues rouges et brunes) et que la consommation d'algues pourrait modifier les niveaux de glucocorticoïdes libérés dans le sang (comme observé chez des agneaux d'élevage : Archer et al. 2007), nous avons aussi recherché si les niveaux de FGM mesurés étaient corrélés à la quantité d'algues ingérée estimée par analyses micro-histologiques dans les échantillons collectés en avril et octobre 2011 et en mars 2012 (n=86 ; Poilvé 2013). Nous n'avons pas détecté d'effets de la consommation d'algues sur les niveaux de FGM. Les trois îles présentaient des niveaux de FGM et des variations saisonnières de FGM similaires, indépendamment des

ressources alimentaires disponibles et de la présence d'activités humaines. Nous avons interprété cette absence de réponse physiologique au stress alimentaire et au risque de prédation par l'existence d'ajustements comportementaux (ex. rythme d'activité en hiver : Parker et al. 1999 ; évitement des zones à risques : Bonnot et al. 2013) et/ou physiologiques (ex. suppression d'une réponse au stress limitant ainsi l'exposition à un stress chronique chez des individus en mauvaise condition corporelle: Taillon & Côté 2008). Il était intéressant de noter que sur toutes les îles les niveaux de FGM culminaient en juillet, interprétable par une plus forte demande énergétique liée à la reproduction [croissance des bois chez les mâles (Pereira et al. 2006) et lactation chez les femelles (DelGiudice et al. 1992)]. Ceci confirmait l'existence de processus physiologiques permettant l'augmentation des niveaux de FGM et appuyait ainsi l'existence d'autres ajustements empêchant le développement de stress chronique lié à une faible disponibilité des ressources alimentaires ou au risque de prédation.

Ce chapitre fut l'occasion de conduire une analyse complémentaire explorant la possibilité d'utiliser des données isotopiques pour estimer la consommation d'algues par les cerfs. Les données disponibles au moment de l'étude ne permettaient pas d'utiliser ces données isotopiques, mais ont permis de soulever quelques perspectives pour de futures analyses qui chercheraient à approfondir cette question.

Chapitre III : Vigilance et stratégie innée de nourrissage sensible au risque chez des cerfs naïfs à la prédation à des stations d'appâts.

-Section 1 : En l'absence prolongée de prédation les cerfs réduisent-ils leur niveau de vigilance et, si oui, quels rôles jouent des niveaux contrastés de nourriture, de lumière et de visibilité ?

Nous avons étudié sur les deux îles sans risque/pauvres (East Limestone et Kunga), en mai et juin 2011 et en mars 2012, les niveaux de vigilance des cerfs à des stations d'appâts équipées avec des pièges photographiques. Nous prédisions que dans ces milieux isolés du risque de prédation les cerfs devraient peu investir dans des comportements anti-prédateurs, telle que la vigilance, et ceci d'autant plus que les milieux sont très abrutis et présentent une faible abondance en ressources alimentaires (Lima & Dill 1990). En outre nous avons également étudié l'effet de la quantité d'appât (élevé/faible), d'un gradient de visibilité (ouverture horizontale du

milieu) et de la période du jour (jour/nuit) sur les niveaux de vigilance. Nous prédisions que, si la vigilance est maintenue, les cerfs devraient être plus vigilants en présence de faible quantité d'appât (peu de gain), à des stations avec une faible visibilité (plus de risque perçu) et la nuit quand la détection visuelle des cerfs peut être limitée par le manque de lumière réduisant alors la visibilité du milieu (Lima & Dill 1990). Malgré plus de 60 ans en absence de prédateurs, les cerfs passaient 9 à 18% de leur temps de nourrissage en vigilance apparente (tête au-dessus des épaules). Ces niveaux de vigilance appartiennent à la tranche inférieure des valeurs publiées dans d'autres études sur des cerfs vivant dans des milieux exposés au risque de prédation. Nous avons exploré quatre hypothèses pouvant expliquer ce maintien de la vigilance avec une emphase sur le rôle des comportements innés (Blumstein & Daniel 2005) et sur le coût des comportements anti-prédateurs, qui, dans le cas de la vigilance, peuvent être réduit si la vigilance est couplée avec d'autres activités tel que le fait de mâcher (Fortin et al. 2004). Cette étude a également renforcé l'importance de considérer le jour et la nuit dans l'étude des patrons de vigilance (Beauchamp 2007) car dans notre étude de cas les cerfs tendaient à être plus vigilants lorsque la visibilité diminuait uniquement la nuit, et les cerfs sur East Limestone étaient plus vigilants le jour, ce que nous avons interprété comme une possible réponse aux activités humaines, plus intenses sur East Limestone (présence de volontaires en mai et juin et de chercheurs en mars) que sur Kunga. Cette étude fut également l'occasion de valider l'utilisation de pièges photographiques pour mesurer le comportement de vigilance chez les cerfs.

-Section 2 : Stratégie innée de nourrissage sensible au risque : les cerfs à queue-noire restent plus effrayés par le loup que par l'ours noir, moins dangereux, malgré 100 ans d'absence du loup

Nous avons étudié sur East Limestone (île sans risque/pauvre) le comportement des cerfs à des stations d'appâts autour desquelles nous avons vaporisé cinq stimuli olfactifs : eau (contrôle neutre), eau de Cologne (contrôle pour une nouvelle odeur neutre), essence (contrôle pour une nouvelle odeur potentiellement répulsive, mis sur du coton), urine de loup (prédateur dangereux) et urine d'ours noir (prédateur moins dangereux car prédateur opportuniste de faons uniquement). Il est important de rappeler que sur East Limestone les cerfs sont isolés de la prédation depuis plus de 60 ans (colonisation d'une île dépourvue d'ours noirs et de chasse), et sont isolés du loup depuis

plus de 100 ans (introduction des cerfs sur l'archipel dépourvu de loup). Nous testions si l'urine de prédateur élicitait des comportements anti-prédateurs innés chez les cerfs étudiés et si ces comportements étaient sensibles au niveau de risque. Si tel est le cas nous prédisions que les cerfs devraient répondre plus fortement à l'urine de loup qu'à l'urine d'ours noir. Pour ce faire nous avons étudié six variables : le nombre de visites, le délai avant la première visite, la probabilité de manger l'appât, le temps passé à la station d'appâts, le temps passé à renifler l'appât et le temps passé en vigilance apparente. En accord avec l'hypothèse d'une stratégie innée de nourrissage sensible au risque, les cerfs répondaient plus fortement à l'urine de loup qu'à celle d'ours noir. Le nombre de visites et le délai avant la première visite étaient le même pour tous les traitements, mais les cerfs passaient plus de temps à renifler en présence d'urine de loup qu'en présence d'urine d'ours noir tous deux supérieurs au temps passé à renifler en présence d'eau. Les cerfs évitaient de manger l'appât et passaient moins de temps aux stations en présence d'urine de loup alors qu'ils consommaient l'appât en présence d'urine d'ours noir. Cependant nous n'avons pas détecté de différence dans le temps passé en vigilance apparente entre les différents traitements. Cette étude suggère qu'en plus d'un évitement inné de se nourrir en présence d'urine de loup, les cerfs auraient plutôt tendance à gérer le risque de prédation spatialement en limitant le temps qu'ils passent dans les milieux risqués plutôt qu'en investissant plus de temps dans la vigilance.

Chapitre IV : Gérer l'interaction cerf-forêt par la peur : test des effets à court terme d'une chasse de faible incidence sur des cerfs naïfs.

Sur Kunga (île sans risque/pauvre), entre avril et juin 2012, nous avons étudié comment une chasse expérimentale pour instiller la peur influençait le comportement de cerfs naïfs à la prédation et comment cela affectait la végétation locale. La chasse fut restreinte à une zone de 21 ha (5% de la superficie de l'île) comprenant le milieu intertidal et la forêt côtière, situés dans la partie sud de l'île. La chasse consista en un maximum d'événements d'effarouchement (tirs à blanc avec ou sans pétards) et trois événements à tirs réels (i.e. 3 cerfs tués représentant moins de 2% de la population de cerfs estimée sur l'île). Ces trois événements semblaient obligatoires pour instaurer un risque assimilable à de la prédation sur cette île dépourvue de prédation sans modifier pour autant la densité de cerfs et donc les ressources disponibles pour chaque cerf. Nous avons traqué les cerfs de jour pendant 11 jours espacés par 3-4 jours ce qui a permis

d'atteindre un effort de chasse similaire à ceux rapportés dans d'autres études de chasse d'ongulés. Nous avons étudié la fréquence de visite des cerfs grâce à des pièges photographiques situés dans le milieu intertidal et à des stations d'appâts placées dans la forêt. Nous avons également suivi la croissance et le taux d'abrouissement de quatre espèces de plantes côtières à croissance rapide. Nous prédisions que les cerfs éviteraient la zone de chasse, et ce d'autant plus le jour qui était la seule période chassée, et que les plantes suivies pousseraient plus et seraient moins broutées dans la zone de chasse que dans la zone non chassée (côte ouest et sud-est de l'île). Les résultats obtenus sur la fréquentation des cerfs dans le milieu intertidal ne permettaient pas de conclure mais aux stations d'appâts seuls les cerfs non marqués (cerfs qui n'avaient jamais été capturés lors de précédentes sessions de captures) évitaient la zone de chasse, alors que les cerfs marqués, ceux qui avaient été capturés au moins une fois, continuaient de visiter les stations d'appâts indépendamment de la période de chasse. Sur les quatre espèces de plantes suivies, la croissance de deux d'entre elles était significativement plus importante dans la zone de chasse que dans la zone non chassée. Ces résultats ont souligné l'importance de considérer le comportement de nourrissage des cerfs et les caractéristiques des plantes en relation avec les plans de gestion avant d'utiliser une chasse destinée à faire peur comme outil de gestion. De plus, le fait que seuls les individus non-marqués évitaient la zone de chasse a mis aussi en évidence l'importance de considérer la variabilité interindividuelle, notamment en termes de comportement répétable (personnalité), et de possibilité d'apprentissage chez les individus. En particulier, ceci a soulevé la question de sélection phénotypique (ex. Darimont et al. 2009 ; Ciuti et al. 2012b) et des conséquences qu'une telle sélection pourrait avoir sur une gestion à long-terme de l'interaction cerf-forêt.

Des données complémentaires sur la réponse physiologique (niveau de FGM) et comportementale (distance d'initiation de fuite à l'approche d'un intrus, niveau de vigilance aux stations d'appâts, patron d'activité et utilisation de la zone de chasse, du milieu intertidal et des zones de chablis) des cerfs à la chasse expérimentale étaient aussi disponibles. Cependant les tailles d'échantillonnage ne permettaient pas de conduire des analyses statistiques et seule une description des patrons obtenus était possible. Ces analyses semblaient globalement confirmer le faible effet de la chasse sur le comportement des animaux marqués. Il est toutefois

intéressant de noter que nous n'avons pas observé d'augmentation de FGM dans la zone de chasse, ce qui pourrait confirmer une gestion du risque par un évitement des zones risquées par les individus percevant du risque. De plus il est possible que les animaux restant dans la partie de l'île où l'expérience de chasse eut lieu, soient globalement plus vigilants de jour comme de nuit pendant la chasse, sauf dans la bande côtière intensément chassée, où les cerfs présents seraient moins vigilants de jour. Ceci pourrait appuyer une gestion spatiale du risque par les cerfs qui, dans les milieux les plus risqués, se concentreraient sur les activités de nourrissage pour réduire leur temps de résidence dans ces milieux plus risqués. Mais ceci reste à valider.

Quelles leçons pour une gestion par la chasse des populations de cervidés dépourvues de prédateurs ?

Ces résultats peuvent être revisités pour tout d'abord éclairer le rôle de la nourriture et de l'absence du risque de prédation dans le maintien de population abondante de cerfs sur les deux îles appauvries en ressources alimentaires et dépourvues de risque que nous avons étudiées. Tout d'abord, l'un des résultats marquant de cette étude est le maintien de bilans énergétiques positifs malgré des milieux très abrutis. Ce résultat peut se discuter à la lumière des premières données démographiques récoltées sur le terrain. Les cerfs de l'étude semblent en effet globalement plus légers et pourraient potentiellement investir un peu moins dans la reproduction que d'autres cerfs à queue-noire évoluant dans des milieux moins appauvris. Ces observations seraient en accord avec une limitation des ressources (Bonenfant et al. 2009). De plus, le climat est globalement doux sur les îles étudiées et la neige y est rare, ce qui pourrait également favoriser le maintien des cerfs dans des milieux très abrutis en limitant l'inaccessibilité des ressources recouvertes par la neige et les coûts de déplacement en hiver. Enfin les cerfs peuvent également consommer des algues qui sont riches en nutriments et qui pourraient avoir des effets bénéfiques sur la reproduction et/ou la survie des animaux (Chapman 1950 ; Allen et al. 2001b). Cependant ces effets ne semblent pas avoir été étudiés sur des ongulés sauvages et mériteraient d'être vérifiés. Ces trois éléments tendent à souligner l'importance des ressources dans le maintien de fortes densités de cerfs. Les coûts épargnés liés à l'absence de prédation semblent moins évidents dans notre étude. Les gains en vigilance semblent limités, mais il est possible que l'absence de prédation relâche les contraintes dans

l'utilisation et la sélection des habitats pouvant alors limiter les coûts de transport et/ou le coût des opportunités perdues si les cerfs devaient éviter des zones risquées. Cependant, ces coûts ne sont pas accessibles dans notre étude et ces aspects mériteraient d'être explorés. Au vu de nos résultats il est possible que l'absence de prédation soit un « facilitateur » permettant le maintien de fortes densités de cerfs, mais la contribution précise de la nourriture et de la peur restent encore à être précisée, notamment par des suivis démographiques à long-terme et par l'étude d'autres comportements anti-prédateurs telle que la sélection fine des habitats et les coûts associés.

Pour finir, j'ai exploré quelles pourraient être les conséquences à long terme de la mise en place d'une chasse qui viserait à limiter l'effet de fortes densités de cerfs dans des milieux isolés de la prédation. J'ai imaginé que pour ce faire les objectifs seraient de maximiser les effets létaux et non-létaux de la chasse tout en limitant les coûts économiques liés à l'effort de chasse. J'ai bâti mon raisonnement à l'aide des résultats obtenus précédemment, et notamment en considérant la réponse contrastée entre les cerfs marqués et les cerfs non-marqués à notre expérimentation de chasse destinée à faire peur (Chapitre IV). En supposant que la majorité des individus rencontrant un chasseur soit éliminée, la chasse sélectionnerait les individus qui éviteraient la zone de chasse. Selon la durée et la fréquence des périodes de chasse et selon l'étendue de la zone de chasse, deux scénarii extrêmes peuvent être envisagés. D'un côté, si l'effort de chasse est maintenu dans une zone restreinte alors les cerfs devraient éviter la zone de chasse et trouver refuge dans la zone non-chassée. Dans ce cas, la végétation dans la zone de chasse pourrait potentiellement se régénérer alors que la végétation dans la zone refuge serait soumise à une plus forte pression d'abrutissement. Une limitation des populations de cerfs dans ces refuges serait attendue par des mécanismes de densité-dépendance. Cependant compte-tenu de l'aptitude des cerfs à s'adapter à des milieux très abrutis et du potentiel des milieux tempérés à maintenir de fortes densités de cerfs (Chapitre I), le devenir de la zone refuge pose de nombreuses questions en termes de biodiversité et de la dynamique locale des populations de cerfs. Dans ce scénario les effets non-létaux de la chasse devraient être maximaux mais l'échelle temporelle à laquelle ils pourraient agir reste à explorer. D'un autre côté, si l'effort de chasse est maintenu sur une zone plus large sans possibilité de refuge, alors

diminuer les effets des cerfs sur leur milieu nécessitera une réduction de la densité de cerfs et dans ce scénario c'est l'effet létal de la chasse qui sera maximal. Bien que ces scénarii soient des cas extrêmes, ils mettent en évidence l'importance de considérer les enjeux et les objectifs de gestion par rapport aux caractéristiques de la population de cerfs (ex. diversité des comportements) et du milieu (ex. ressources disponibles pour les cerfs) à gérer. De nombreux défis restent à relever dans la gestion des fortes densités de cerfs mais puisque dans le passé « nous avons su être des gestionnaires de cerfs efficaces » (Woolf & Roseberry 1998) dans une optique de restauration des populations, il y a de bonnes raisons de penser que « nous » saurons dépasser ces défis et continuer à être « des gestionnaires de cerfs efficaces ».

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For you, dear reader:

Thank you for opening this manuscript concerning the relationship between deer, food and predation risk in heavily browsed environment. The present document is organized around four questions. Each question is addressed in a specific chapter which consists in two parts: first, the main response assessed for a given question corresponds to one or two scientific articles that have been or will be submitted. They may include appendices and/or supplementary materials. The state of the article and the journal targeted are provided in the front page of each chapter. Second, for three chapters, you will have access to complementary analyses which provide both contextual information and additional results in order to better assess how deer manage predation risk in heavily-browsed environments. To conclude this foreword, it remains for me to wish you a pleasant reading.

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“One of the biggest flaws in the common conception of the future is that the future is something that happens to us, not something we create.” – Michel Anissimov

“Un des plus grandes défauts dans la conception courante du future est de croire que le future est quelque chose qui nous arrive, et non pas quelque chose que nous créons.” (traduit par mes soins)

INTRODUCTION

We are witnessing a massive loss of biological diversity with current rates of species extinction at least 100 times higher than the typical rates through Earth's history (Pimm et al. 1995). All kinds of ecosystems, ranging from wetlands and marine ecosystems to grasslands and forest ecosystems are exposed to human-induced threats including land-use changes, invasive alien species, environmental pollution and resource over-exploitation (WRI 2000; Alessa & Chapin 2008; IUCN 2013; Yule et al. 2013). Despite sustained conservation efforts, biodiversity is still expected to decline (Pereira et al. 2006; Dullinger et al. 2013; Aslan et al. 2013). In particular, in 2013 the International Union for Conservation of Nature (IUCN) estimated that at the global scale, among the species assessed, one in eight birds, one in five reptiles, one in four mammals and one in three amphibians are currently threatened with extinction (Böhm et al. 2013; IUCN 2013).

Strikingly, in the meantime, at the local scale other species have increased in abundance, especially among large herbivores (e.g. McShea et al. 1997; Gordon et al. 2004; Danell et al. 2006) to the point of being identified as “overabundant”. In large sections of North America and Europe, this resulted in a loss of understory plant cover and diversity with cascading effects on animal diversity, dramatic changes that, at first sight, did not prevent herbivores from maintaining high local densities (Figure 1).

The present study focuses on this apparent paradox and investigates how large herbivores, like deer, can adjust to the habitat changes they have caused and the role the absence of predation risk plays in the ability to adjust to habitat simplification (Figure 1).

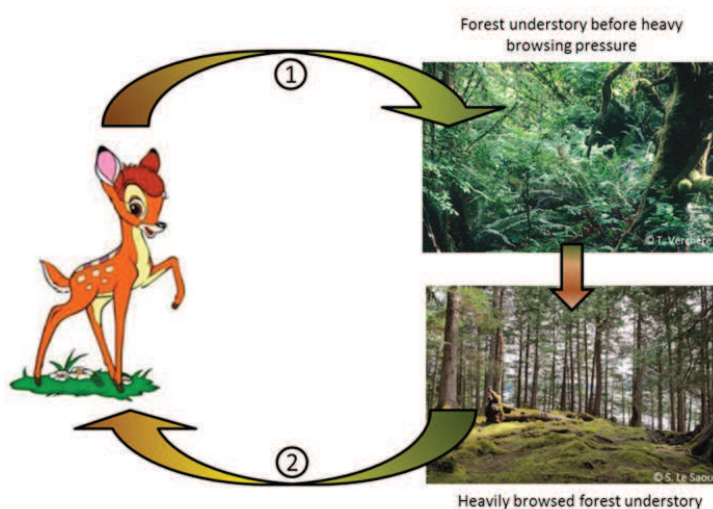


Figure 1: Schematic relationship between deer and their environment. (1) Highly abundant deer populations affect their environment in reducing the forest understory abundance and diversity, among others. (2) Deer are then leaving in a depleted environment that they have created themselves and have to adjust to this new environment. Both links are required to assess a complete view on the relationship between deer and their environment. The present study focuses on this second interaction.

I. A BRIEF REVIEW OF DEER IN THE WORLD

I.A. DEER OVERABUNDANCE: LOCAL ISSUE COMMON AT A GLOBAL SCALE

Within the last 50 years, some populations of large herbivores have dramatically increased locally. They may even have exceeded historical records of density and are often qualified as “overabundant” (McShea & Rappole 1997). Overabundance is a judgment value which is context-dependent and because the term “overabundance” may be subjective, it should be used with cautions (McShea & Rappole 1997; Sinclair 1997). For Caughley (1981), populations have been considered overabundant because they threaten (i) human-life or livelihood, (ii) a favored species by depressing its density, (iii) their own good or (iv) the functioning of an ecosystem. Only the latter case should be considered as ecological overabundance (Caughley 1981). Such alteration of ecological functions may often be severe enough to call for management.

Among these species, deer (i.e. *Cervidae*, *Moschidae* and *Tragulidae* species) are a peculiar example (Box 1). Severe impacts of high-density deer populations on their environment have

been reported for at least 15% of deer species in the world, such as sika deer (*Cervus nippon*) in Japan (Takatsuki 2009), red deer (*Cervus elaphus*) and sika deer in New Zealand (Nugent et al. 2001), roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) in Europe (e.g. Gonzalez Hernandez & Silva-Pando 1996; Pellerin et al. 2010) or white-tailed (*Odocoileus virginianus*) (e.g. Rooney & Waller 2003) and black-tailed deer (*Odocoileus hemionus*) in North America (e.g. Opperman & Merenlender 2000; Martin et al. 2010)(but see Coté et al. 2004, Chollet 2012 for reviews; Box 1).

BOX 1: DEER IN THE WORLD

Deer¹ are ungulates² and belong to the ancient Artiodactyla order (from Greek “*ártio*” for “even” and “*dáktylos*” for “finger or toe”) today regrouped with the ancient Cetacea order (marine mammals, from Latin “*cetus*” and Greek “*ketos*”, “whales”) within the Cetaceartiodactyla order. Deer encompass three families: Cervidae (true deer), Moschidae (musk deer) and Tragulidae (mouse deer) (Wemmer 1997).

There are 72 deer species, among which Pere David’s deer (*Elaphurus davidianus*) persists only under captive management in China (extinct in the wild: IUCN 2013) and Schomburgk’s deer (*Cervus schomburgki*) does not exist anymore (recognized as extinct since 1994: IUCN 2013). About 50 deer species (c. 70%) occur mostly in tropical areas (below 33° latitude) among which 48% are threatened and 18% have unknown status (Data deficient : IUCN 2013) (adapted from Wemmer 1997 with IUCN 2013 data)(Figure B1). On the contrary, among the 15 species (21%) which occur mostly in temperate and boreal areas, at least 40% present some high-density populations locally causing socio-economic and ecological issues locally and may thus be considered as overabundant (sensu Caugley 1981) (Figure B1, Table B1). Some locally overabundant deer populations also occur in tropical areas, for both native (e.g. sika deer – *Cervus nippon*- in Japan) and introduced deer species (e.g. Philippine deer – *Cervus mariannus* - in Guam, Marianne Islands, Figure B1, Table B1). Remarkably, although locally

overabundant, at the global scale their status may differ: indeed, among the eleven species identified as overabundant locally, 4 (36%) are increasing population at the local scale, 3 (27%) are stable at the global scale, and 3 other ones are decreasing in their native range but overabundant where introduced (e.g. rusa deer or Reeve’s muntjac, see Table B1).

Deer are thus an interesting model presenting contrasted trends at both global and local scales, and both among species (from threatened to least concern; IUCN 2013) and within species (from locally declining to locally overabundant; Table B1). This has aroused a strong interest in the science community and has resulted in a large body of studies and experiments investigating how deer interact with their environment within a wide variety of local contexts. A review of this work can help to improve local deer management by providing an opportunity to learn from the dynamics of other deer populations worldwide (e.g. Nugent et al. 2011).

¹ *Deer comes from the Old English “*deor*” that means “animal, beast”, stemmed from the Proto-Germanic word “*deuzam*” meaning “animals” in opposition to “man”. In Latin languages, *cerf* in French, *cervo* in Italian and Portuguese, or *ciervo* in Spanish, come from the Latin word “*cervus*” stemmed from the Indo-European root “*ker-*” or “*kor-*” which means “protuberant feature”, in reference to their antler. “*Cervus*” is thus the group of animals with antlers. (Le Robert, Dictionnaire Historique de la Langue Française)

² **Ungulate comes from the Latin “*ungula*” that means “nail” and by analogy “hoof, claw, talon”. Ungulate designs thus the group of “hoofed animals”.

BOX 1 (continued)

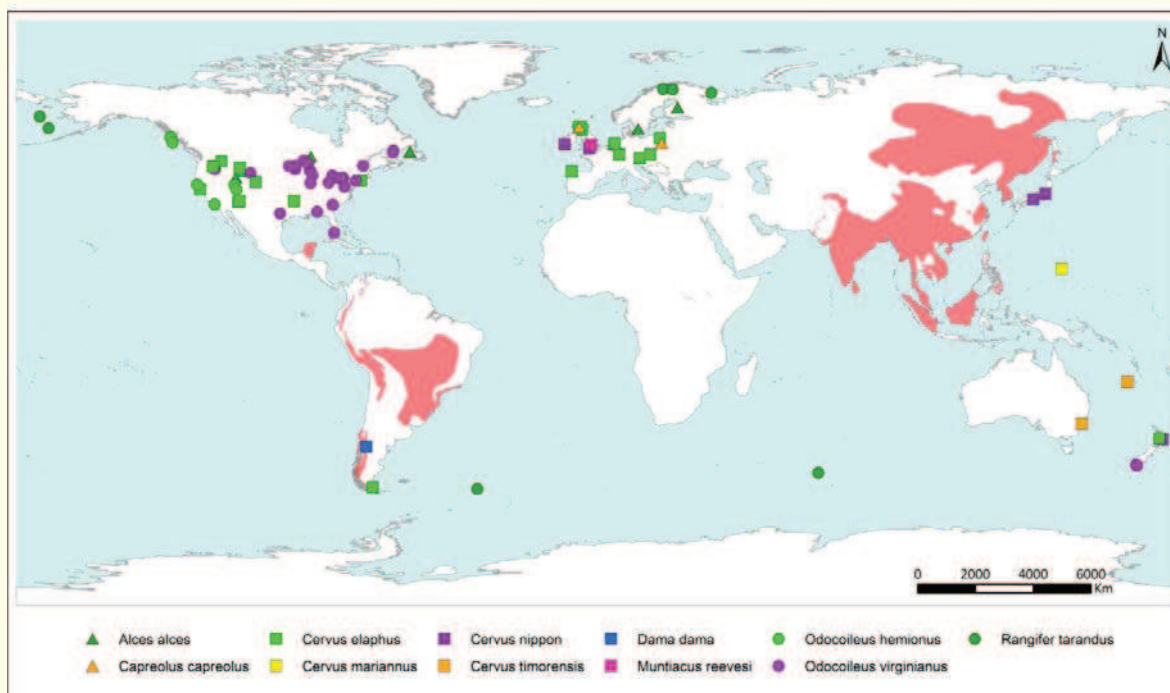


Figure B1: Deer in the world: location of threatened species and overabundant populations. The extents of occurrence of the 32 threatened species are mapped by red areas. Reviewed overabundant populations of deer (Table B1) are localized by dots in relation to the species considered.

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BOX 1 (continued)

Table B1: Brief review of the main cases of deer overabundance reported in the world according to the origin of deer populations (native or introduced). For context, the species conservation status (Least Concern or Vulnerable) and population trend at the global scale (↗: increasing; =: stable; ↘: decreasing; and ?: unknown) are presented according to IUCN 2013. This review does not pretend to be exhaustive, but provides an overview on the situation of overabundance in the world. This review is adapted from Chollet 2012.

Code	Species	Native	Introduced	Global conservation status and population trend (IUCN 2013)
▲	<i>Alces alces</i> (moose)	Finland: ^{1,2} Poland: ³ Sweden: ⁴ USA: ⁵⁻⁷	Canada: ⁸	Least Concern ↗
▲	<i>Capreolus capreolus</i> (roe deer)	Czech Republic ⁹ France ¹⁰ Germany ¹¹ Netherlands ^{12,13} Poland ³ Spain ¹⁴ Sweden ⁴ Scotland ¹⁵		Least Concern ↗
■	<i>Cervus elaphus</i> (red deer, elk)	Czech Republic: ⁹ France: ¹⁰ Germany: ¹¹ Netherlands: ^{12,13} Scotland: ¹⁶ USA : ^{7,17-28}	Chili: ²⁹ New Zealand: ^{30,31} Spain: ¹⁴ Victoria Island: ³²	Least Concern ↗
■	<i>Cervus mariannus</i> (Philippine deer)		Guam, Marianne Islands: ³³	Vulnerable ↘
■	<i>Cervus nippon</i> (sika deer)	Japan: ^{34,35}	Ireland: ³⁶ New Zealand: ^{30,31} England: ³⁷	Least Concern ↗
■	<i>Cervus timorensis</i> (Rusa deer)		Australia: ³⁸ New Caledonia: ³⁹	Vulnerable ↘
■	<i>Dama dama</i> (fallow deer)		England: ³⁷ Victoria Island, Canada: ³²	Least Concern ?
●	<i>Odocoileus hemionus</i> (mule-, black-tailed deer)	USA: ^{7,40,41}	Canada (Haida Gwaii): ⁴² USA: ⁴³	Least Concern =
●	<i>Odocoileus virginianus</i> (white-tailed deer)	USA: ^{5,7,23,44-66}	Canada: ^{67,68} New Zealand ^{69,70}	Least Concern =
●	<i>Rangifer tarandus</i> (caribou, reindeer)	Finland ^{71,72} Norway: ⁷² Russia: ⁷³	Kerguelen Islands: ⁷⁴ South Georgia: ⁷⁵ USA: ^{76,77}	Least Concern =
■	<i>Muntiacus reevesi</i> (Reeve's muntjac)		England: ³⁷	Least Concern ↘

I.B. WHY DID DEER BECOME HIGHLY ABUNDANT IN TEMPERATE ENVIRONMENT?

During the last century major changes in land-use occurred (Vitousek et al. 1997; WRI 2000; Foley et al. 2005) providing favorable habitats for deer populations. In particular, the increase in crop and/or logged areas in North America (e.g. review in McShea et al. 1997; Waller 2008; McShea 2012) and Europe (e.g. Hewison et al. 2001; Wilson et al. 2009; review in Côté et al. 2004; Clutton-Brock et al. 2004) created suitable habitats for deer rich in high-quality food (i.e. high-energy content). The decrease of human activity in mountain areas played a role in many parts of the world as illustrated in Japan for sika deer (review in Takatsuki 2009). In addition, supplementary winter feeding became common in most European and North-American countries with a long tradition of game hunting and/or with high deer winter mortality (e.g. review in Baker & Hobbs 1985; Putman & Staines 2004).

Concomitantly, hunting pressure decreased due to both a reduction in hunter populations and in hunting quotas as well as to hunting regulations promoting male hunting in favor of doe and fawn survival (review in Côté et al. 2004; Tanentzap et al. 2012). In addition, by the early 20th century, humans had extirpated most native predators of deer [e.g. wolves (*Canis lupus*), cougars (*Puma concolor*), wolverines (*Gulo gulo*)] (e.g. in Europe & North America: review in Waller 2008).

I.C. ECOLOGICAL IMPACTS OF OVERABUNDANT DEER

Deer impact on the composition and structure of plant communities has been extensively studied (e.g. review in Hanley 1993; Stromayer & Warren 1997; Waller & Alverson 1997; Gill 2000; Russell et al. 2001; Augustine & DeCalesta 2003; Stockton et al. 2005). For example, in Northwestern Pennsylvania, US, Rooney & Dress (1997) reported that in presence of high-density populations of white-tailed deer, old growth forests lost over 50% of plant species in 66 years with major changes in the local forest ecosystem. In addition, high-density population may also have indirect effects on the plant community in altering nutrient cycle (e.g. N cycle: Ritchie et al. 1998; review in Pastor et al. 2006), soil characteristics (e.g. trampling: Nomiya et al. 2003) or tree vigor (e.g. bark-stripping: Akashi & Nakashizuka 1999; but see Gill 1992 for a review of

deer damage). Understanding these intricate indirect effects of deer on their environment have opened a new research avenue that still need further investigation (Weisberg & Bugmann 2003; Hunter et al. 2012).

Such changes in the structure and composition of forest understory may in turn affect other animal communities. For example, deer impact on the local avifauna was reported in boreal (e.g. Cardinal et al. 2012) and temperate forests (e.g. deCalesta 1994; Allombert et al. 2005a; review in McShea & Rappole 1997; Fuller 2001; Chollet & Martin 2012). Insect communities can also be affected by deer as observed in boreal (e.g. Suominen 1999; Suominen et al. 1999), temperate (e.g. Feber et al. 2001; Allombert et al. 2005b) and subtropical environments (e.g. Barrett & Stiling 2007). For a review on deer impacts on forest ecosystems see for instance Rooney (2001) and Côté et al. (2004). Consequently, due to both deer direct and indirect effects on their environment, deer has been sometimes considered as “ecosystem engineer” (Côté et al. 2004): i.e. a species that “modifies, maintains and creates new habitats” (Jones et al. 1994). Within this framework, deer management has become a main concern in wildlife management (review in Côté et al. 2004) in protected areas (e.g. Ripple & Larsen 2000; Keith & Pellow 2005) as well as in logging (e.g. Wiggins 1996; Ward et al. 2004) or suburban and urban areas (e.g. Urbanek et al. 2011; Williams et al. 2012).

I.D. SOCIO-ECONOMIC IMPACTS OF OVERABUNDANT DEER

On top of these ecological consequences, abundant deer populations have also caused increasing socio-economic issues, which strengthen the need for adaptive management plans. Indeed, heavy deer-browsing pressure may dramatically reduce tree regeneration (e.g. Watson 1983; Frelich & Lorimer 1985; Vila et al. 2003a, 2003b). This in turns may have detrimental consequences on forestry industry which annual economic lost was estimated to be \$ 367 million in Pennsylvania’s Allegheny hardwood forest in the 1980s (Conover et al. 1995). Similarly, deer browsing and damage on field crops (e.g. corn, hay) in the United States represented a total economic loss of \$274 million for farmers in 1994 (Wywiałowsky 1994 in Conover et al. 1995). In addition, abundant deer populations may also use urban and suburban areas as predator refuges (e.g. Burcham et al. 1999) and/or as foraging area (e.g. home

gardening and landscape planting: Curtis & Richmond 1994; review in DeNicola et al. 2000). This increasing proximity between humans and deer has resulted in high rate of deer-vehicle collisions, estimated to be over a million collisions per year in the United States with over 200 human deaths attributed to these events (Conover et al. 1995). Finally, increasing the number of human-deer contacts may also promote zoonoses (i.e. human disease caused by infectious agents transmitted by animals: Acha & Zyffres 1988 in Wilson & Childs 1997). This was indeed suggested by positive correlation between deer density and risks of contracting Lyme disease in the United States (Stafford et al. 2003; Paddock & Yabsley 2007). A better understanding of the relationships between deer and their environment appears thus critical.

II.POPULATION LIMITATION : A LITTLE BIT OF THEORY

II.A. CONCEPTS AND SCIENTIFIC DEBATES

II.A.1.LIMITATION, DENSITY-DEPENDENCE AND REGULATION CONCEPTS

Population limitation means that the population growth is constrained. Any factors which affect the mortality and/or reproduction rates of a given population are thus limiting factors (Sinclair 1989; Messier 1991; Sinclair & Pech 1996). Limiting factors may be intrinsic (i.e. characteristics of individuals within a population such as individual genes, behaviors and physiology) or extrinsic (i.e. external to the individuals). Generally four kinds of extrinsic limiting factors are considered: resources, predation, disease and chemo-physical environment (e.g. climate, geologic changes)(Sinclair 1989). These factors may act independently or in synergy at a given time with different relative importance at different time (Sinclair 1989).

Limiting factors may be density-dependent or density-independent. Density-dependence refers to processes which mechanism and/or intensity vary with the population density. In opposition, density-independent processes are not affected by the population density (Fowler 1987; Sinclair 1989, 2003). A classic example of density-dependent factors are resources since the level of resources available decreases as the number of users increases and become thus even more limiting. On the contrary, weather conditions (e.g. snowfall) may be more or less intense independently from animal abundance (e.g. Sinclair 1989, 2003). The intensity of density-

dependent relationships depends on the kind of limiting factors and on the species considered. This relationship may vary among years and/or populations exposed to different sets of limiting factors as well as among individuals (e.g. sex and/or age-specific relationship) (e.g. review in Fowler 1987; Sinclair & Pech 1996; Turchin 1999; Eberhardt 2002; Sibly et al. 2005; Bonenfant et al. 2009). Note that predation, like disease, may be density-dependent or density-independent given the context, whereas natural resources are ultimately density-dependent and chemo-physical environment are density-independent (Messier 1991; Sinclair 2003).

Population regulation is a temporal process and means that there is a mean level of density around which a population fluctuates over time without “wandering far away” from this “equilibrium” (Turchin 1995). The concept of equilibrium should be understood as a “cloud of points” or range of values towards which the population density tends to return (Turchin 1995). Another elegant way to describe the notion of equilibrium could be the analogy with a stream and the population density would be something which tries to remain at the center of the stream (J. Cohen, Intecol 2013). Any density-dependent factors, which ultimately keep a population within its normal range of density (center of the stream) without excessive time lag, are regulating factors (Sinclair 1989; Messier 1991; Turchin 1995, 1999). Regulating factors are thus a subset of limiting factors involved in short- or medium-term negative feedbacks on a population density and generating a “return tendency” toward the equilibrium (Sinclair 1989; Messier 1991; Turchin 1995, 1999). The notion of equilibrium and the processes involved in population regulation have been largely debated (e.g. review in Sinclair 1989; Turchin 1995, 1999; Bonenfant et al. 2009) and the subject is not dried up yet (e.g. Ziebarth et al. 2010; McGill 2013).

Whether regulation may exist during a given temporal window and how it occurs, is a whole theme of research in itself and is out of the scope of the present study. Here, instead we considered only potential limiting factors that may affect deer population and pay a special attention to food as resource and predation risk. Other resources (e.g. water, thermic cover), disease and chemo-physical environment will not be detailed directly but will be considered when interacting with food level or predation risk and considered as environmental characteristics.

II.A.2. BOTTOM-UP AND TOP-DOWN CONCEPTS

In the meantime to the debate on whether population regulation exists and how it occurs, another debate animated the scientific community which tried to assess whether food or predation was the main limiting factor. From a trophic perspective, population may be limited by two complementary mechanisms: bottom-up (i.e. limitation by food: Huston 1979) and top-down controls (limitation by predation: Hairston et al. 1960). Both hypotheses pitted against each other for decades (e.g. Power 1992; Polis 1999; Terborgh et al. 2001; Sinclair & Krebs 2002; review in Stolzenburg 2009), but are now both recognized as affecting population dynamics and their relative importance is context-dependent (Hunter & Price 1992).

In addition, the use of linear trophic chain (i.e. predator interacting with herbivore interacting with plants) has also been reconsidered. Currently, instead of a “chain”, scientists generally recognize that life beings are connected in a “network” or “web” with multiple interactions among and within trophic layers which may be direct (effect of agent A on agent B via agent A) or indirect (effect of agent A on agent B via a third agent C) (Polis & Strong 1996; Polis et al. 2000; Abrams 2005; Ohgushi et al. 2012). Within this context, a better understanding of the mechanisms by which food and predation may affect a given population remains a topical question (Estes et al. 2011; Ohgushi et al. 2012).

II. B. FOOD AS LIMITING FACTOR: HOW DOES IT AFFECT DEER POPULATION?

II.B.1. DEER DIET, SURVIVAL AND REPRODUCTION

Deer are large herbivores which feeding style may be classified under three categories (Janis 1988 in Danell et al. 2006): (i) grazer feeder, like Pampa’s deer (*Ozotoceros bezoarticus*), swamp deer (*Cervus duvaucelii*) or Eld’s deer (*Cervus eldii*), which include over 90% of monocotyledons^{3*} in their diet (i.e. feeding mostly on grasses and monocotyledonous forbs); (ii)

³ * Cotyledon comes from the ancient Greek “kotylê” – hollow things - and refers to the lobule of mammalian placenta and by analogy to the embryonic leaves of plants. Dicotyledons are a group of plants which seedlings have two cotyledons, in contrast to monocotyledons which have a single cotyledon.

browser or concentrate feeder, like muntjac (*Muntiacus muntjak*), moose (*Alces alces*), roe deer (*Capreolus capreolus*) or brocket deer (*Mazama sp.*), which include over 90% of dicotyledons* in their diet (i.e. feeding mostly on tree and shrub foliage, forbs and fruits); and (iii) mixed feeders, like black- and white-tailed deer, sika deer, red deer or Rusa deer (*Cervus timorensis*), which include intermediate proportions of dicotyledons and monocotyledons in their diet. Remarkably, grazer feeders seem more vulnerable to habitat changes, whereas browser and intermediate feeders seem to be more tolerant to anthropogenic modifications of their habitats (Wemmer 1997). In particular most species with overabundant populations (Box 1) are browser or intermediate feeders (Wemmer 1997) and seem to cope well with human-dominated mosaic landscapes with crops (high energy food) and forests (refuges) (e.g. Hewison et al. 2001; review in Côté et al. 2004)

Deer are selective feeder and alternate the relative proportion of different food items according to seasonal changes in plants (e.g. in black-tailed deer: Parker et al. 1999; in red deer: Dumont et al. 2005; in reindeer : Thompson et al. 2010; in roe deer: Barančková et al. 2012). In particular, deer select their diet based on both the quantity and the quality of available forage (e.g. Klein 1990; Parker et al. 1999; Van der Wal et al. 2000; Bergvall 2007; Wam & Hjeljord 2010).

Reduction in either food quantity or quality can have detrimental effects on deer survival. For example, the elimination of lichen from St Mathew Island is likely to have caused reindeer starvation in interaction with severe winter conditions (Klein 1959). Similarly, survival rate of elk females in the Rocky Mountains depends on winter climatic conditions, winter nutrition as well as on body fat at the beginning of winter (Cook et al. 2004). Storing energy as body fat during the high-productivity season (i.e. summer-fall in temperate environment) is a common strategy in deer living in habitats where the food available during the low-productivity season (i.e. winter in temperate environment) will never meet deer energy demand. For these species, forage quantity and quality during the high-productivity season is critical for deer survival (e.g. in moose: Moen et al. 1997; in black-tailed deer: Parker et al. 1999; review in Moen et al. 2006).

Food is also a major limiting factor in deer reproductive success. For capital breeders (Jönsson 1997), like reindeer, the energy stored in summer is the critical factor determining reproduction success during the following spring. Indeed, reindeer give birth slightly before the spring flush and hence the initial post-natal care relies heavily on the body reserve of the mother (Reimers et al. 1983; Flydal & Reimers 2002). On the contrary, for income breeders (Jönsson 1997), like roe deer, the spring flush is the critical factor, because birth occurs concomitantly with the spring flush and roe deer do not build body reserve (Andersen et al. 2000). However, whatever strategy deer adopts, food quantity and quality affect deer diet (i.e. botanical composition) and nutrition (i.e. the relation between the supply and the requirement of energy and nutrient: McLaren 1988 in DelGiudice 1995) and have a critical impact on deer reproduction (review in Parker 2003).

II.B.2. PLANT-MEDIATED FEEDBACK ON DEER POPULATION

As selective feeders, deer deplete first their preferred food (Augustine & McNaughton 1998). This results in habitats with a higher proportion of less preferred food (e.g. Tilghman 1989; Horsley et al. 2003). As a result, deer populations adjust their diet and include an increasing proportion of less-preferred forage (e.g. Maizeret et al. 1989). For instance, on Anticosti Island, where for over 100 years introduced white-tailed deer have reduced by half the cover of balsam fir (*Abies balsamea*), a favorite item in their winter diet (Potvin et al. 2003), deer increased their consumption of white spruce (*Picea glauca*), a much less-preferred food items (Sauve & Cote 2007). Similar shifts in diet have been observed in most studies in depleted environments, including shifts towards litterfall subsidies (e.g. sika deer in Japan: Takahashi & Kaji 2001; white-tailed deer in Canada: Tremblay et al. 2005) or marine resources accessible at low tide (e.g. red deer feeding on brown and red algae on the Isle of Rum, Scotland: Conradt 2000).

Because plant nutritional value is a critical component of deer's energy balance, shifts in their diet caused by self-induced food depletion may be expected to affect deer survival and/or reproduction (Robbins 1993; Parker 2003; Parker et al. 2009). Indeed, less-preferred food are generally less palatable food (e.g. Koda & Fujita 2011) containing various concentrations of protein, fibers and secondary components, like tannins (Hanley 1982). Tannins are phenolic

components which reduce dry matter and sometimes protein digestibility (Robbins et al. 1987a, 1987b). Some deer, like fallow deer (*Dama dama*) have been reported to avoid plant items rich in tannins (Bergvall 2007). Shifting from preferred to less-preferred food may thus, at least in some cases, be synonymous of a shift from high-quality (e.g. low-tannin content) to low quality (e.g. high-tannin content) plants. Such a shift would be expected to reduce deer nutritional balance and hence could affect deer survival and reproduction (Parker 2003; Parker et al. 2009). However, deer may also adjust their food intake (bite rate and bite size) in response to change in food quantity and quality (Trudell & White 1981; Wickstrom et al. 1984). Plant nutritional value for deer may also vary seasonally (both intrinsically and possibly during the digestion process: Hanley 1982; Robbins et al. 1987b; Parker et al. 1999). Note that, in response to herbivory, plants may also synthesize chemical defenses decreasing plant palatability and nutritional value for deer (Augustine & McNaughton 1998; Vourc'h et al. 2001). Detailed studies of deer nutrition are thus required to accurately assess how changes in diet may affect deer nutritional balance and how this may translate at the population level (Hanley 1982; Robbins et al. 1987b; Robbins 1993; Parker 2003; Parker et al. 2009).

In addition, concomitantly to shifting their diet and the associated energy supply, deer may also alter their behavior and the associated energy requirement (Clutton-Brock et al. 1987; Parker et al. 1999). For example in response to reduced food levels deer may use different habitats (e.g. Clutton-Brock et al. 1987; Tufto et al. 1996; Conradt 2000). This may be associated to various behavioral adjustments (e.g. change in activity pattern) and may interact with other limiting factors such as changes in environmental characteristics (e.g. thermic cover) and/or predation risk (Conradt 2000). These changes are likely to result in different energy requirements. Due to intricate relationships between deer energy supply and requirements which may vary as a function of deer diet composition and habitat use, weather condition and predation risk, as well as of deer sex and age class, understanding how deer respond metabolically to changes in their food resource remains an interesting research avenue (Parker 2003; Parker et al. 2009).

Although the fine metabolic mechanisms may not be totally described yet, the impact of deer-induced food depletion (density-dependent food limitation) on deer demographic parameters has been well studied (review in Bonenfant et al. 2009). In particular, Eberhardt's model (2002)

predicts the following sequential effect of increasing food limitation on deer demographics: 1) impact on juvenile survival, 2) impact on age at first reproduction, 3) impact on adult reproductive rate and 4) impact on adult survival. In their review, Bonenfant et al. (2009) concluded that most of these prediction were validated in deer populations subject to density-dependent food limitation. In particular, they showed that most food-limited deer populations are subject to higher juvenile mortality and show a delay in age at first reproduction in females. This emphasizes the strong impact of food as a limiting factor in deer population.

However, this is not always the case. For example, on Anticosti Island, high-density populations of white tailed deer (> 20 deer/km²) have dramatically depleted their environment for over 100 years impacting thus their food supply and triggering significant changes in their diet (Potvin et al. 2003; Tremblay et al. 2005). Regarding survival rate, Taillon et al. (2006) studied the impact of low-quality winter diet on fawn survival. They fed fawns with either the local diet selected by wild fawns in winter, or with an impoverished diet containing a higher proportion of white spruce, a species deer normally avoid. Fawns fed with the impoverished diet had a similar winter survival rate than fawns fed with the normal diet. However, during the same experiment, Taillon & Côté (2007) showed that fawn fed with the impoverished diet reduced their aggressiveness levels whereas control fawns did not. This suggests that fawn may have modified their behaviors in a way ensuring their survival. With respect to reproductive rate, Simard et al. (2008) compared the body mass and the number of ovulations in adult females between the current deer population and the one from 30-years ago. They showed that does were 6% heavier 30 years ago but had similar ovulation number. This suggests that deer can modify their life-history strategies to maintain reproduction at the expense of growth.

These results highlight the remarkable ability of deer to cope with their self-induced depleted environment and pinpoint the complex interactions that may occur between deer behavior and physiology in relation to their environment. Here I presented a single case of these interactions, however see Bonenfant (2009) for a comprehensive review on how sex, age and climate, to cite a few, may also interact in affecting deer demographic response to self-induced food restriction. More studies are thus required to better assess the ins and outs of the network of interactions between deer, food and environmental characteristics.

Until now, we have focused on deer as a “plant predator” and seen how plant-prey may alter deer population dynamic. However, deer are also a prey and for this reason they also have to deal with predation pressure when intending to change their behaviors. We are now considering how predation may affect deer population

II.C. PREDATION AS LIMITING FACTOR: HOW DOES IT AFFECT DEER POPULATION?

II.C.1. CONSUMPTIVE EFFECTS OF PREDATION

By definition, predation means acquiring and consuming a prey. It impacts thus prey survival directly via this consumptive effect (e.g. Preisser 2009), also referred as “lethal effect” (e.g. Creel & Christianson 2008), “numerical effect” (e.g. Rooney & Anderson 2009), “density-mediated interaction” (e.g. Preisser et al. 2005) or “N-driven effect” (e.g. Brown et al. 1999; Orrock et al. 2012). However, the extent to which predation may limit prey density is not trivial (Gese et al. 2001; Sinclair & Krebs 2002). Overall, one of the main difficulties in identifying predation effects on prey demography is to determine whether predation is an additive or a compensatory cause of mortality. Additive mortality occurs when an increase (or decrease) in a factor increases (or decreases) the overall mortality rate of a given population. Compensatory mortality occurs when an increase (or decrease) in a factor does not change the overall mortality rate (Connolly 1981; Boyce et al. 1999). Within this framework, predation is an effective limiting factor if it is an additive but not a compensatory mortality source.

For example, in Alaska, U.S., Gasaway et al. (1983) showed that reducing wolf abundance enhanced moose survival rate and led to an increase in the local moose population. They concluded that wolf limited the moose population. Similarly, Messier & Crête (Messier & Crête 1985) showed that moose predation by wolves and maybe black bears (*Ursus americanus*) limited low-density moose populations in Québec, Canada (but see Messier 1991 's introduction for a review of cases where predation was identified as a limiting factor on moose populations).

However, natural predators, especially chasers, are more likely to select for animals in poorer conditions (e.g. parasitized, injured, malnourished, younger or older individuals: Boyd et al. 1994; review in Mech & Peterson 2003; Barber-Meyer & Mech 2008) which might not have

survived in any cases. Indeed, in a review of the effects of predator removal on black-tailed deer, Forrester & Wittmer (2013) reported only a single study out of the seven reviewed that showed a clear increase in the growth rate of the predated deer population (additive mortality), whereas four studies (58%) showed no changes in deer population growth rate (compensatory mortality), and the last three showed no clear conclusions. Another striking case was reported in North Western Colorado, U.S., where Bartman et al. (1992) showed that a reduction in coyote (*Canis latrans*), the main predator of mule-deer fawn in the area, did not affect the overall mortality rate of fawn. Indeed, even if the amount of fawns killed by coyote decreased, the number of fawns starved to death increased compensating the reduction in coyote predation. Similarly, although the reintroduction of the wolf in the Yellowstone National Park was followed by a decline of c. 8%/year in the elk herd between 1995 and 2004, modeling including weather conditions and human harvest but not wolf predation predicted a decline of c. 7.9%/year in the elk population. This suggested that during the temporal window studied wolves were likely a compensatory limiting factor.

Predation as a compensatory limiting factor seems to be frequent in abundant deer populations exposed to harsh winter conditions (e.g. Mech et al. 1987; Keech et al. 2011; review in Boyce et al. 1999; Andersen et al. 2006) what supports Messier et al.'s (1991) predictions. In their model, Messier et al. considered a single and reciprocal prey-predator relationship. Although providing a simplified view of most real systems, their model show that in situations with low prey densities, predation is likely to be the primary additive mortality factor limiting prey population. In this case, it may even act as a regulating factor. However, in situations with high density of prey, prey consumption by predator is behaviorally and physically limited by the time predator can devote to foraging and the time they need to handle a prey (i.e. detect, capture and consume). In this case, prey are more likely to be primarily limited by food resource in interaction with environmental characteristics (climate, disease).

Interestingly, these conclusions may still be relevant in systems involving humans as predator (i.e. hunting). Hunting is rarely, if ever, compensatory due to the kind of animals targeted (e.g. big male for trophy hunt, protection of fawns and does under some hunting regulations: Milner et al. 2007). However, the global trend discussed by Messier et al (2001) is still validated. In

systems where deer abundance is relatively low in comparison to hunting pressure (i.e. number of animal harvested), hunting can limit deer population (e.g. Kilpatrick et al. 1997; Kilpatrick & Walter 1999; Nugent et al. 2001, 2011; Collins & Kays 2011) and may even threaten the persistence of some species (e.g. musk deer in China: Zhou et al. 2004; review in Milner et al. 2007). On the contrary, in systems where deer abundance largely exceed deer harvest rates, hunting has little numerical impact on deer abundance (e.g. Nugent et al. 2011; Simard et al. 2013). The consumptive effect of predation as the main limiting factor seems thus to be context-dependent.

So far we considered only the consumptive effect of predation which may affect deer population dynamics by reducing the number of deer (Figure 2). However, since 1990s an increasing amounts of studies showed that predation has also a non-consumptive effect which may affect prey demography by inducing behavioral and/or physiological changes (Lima 1998b; Preisser et al. 2005; Creel & Christianson 2008, Box 2, Figure 2). In particular, some remarkable experiences showed that the presence of inoffensive predators, which ability to kill was eliminated, could reduce prey survival and/or reproduction (e.g. Peckarsky et al. 1993; Schmitz et al. 1997; Nelson et al. 2004; review in Newman et al. 2013). For example, Schmitz et al. (1997) showed that grasshoppers in presence of spiders with glued mouth had the same mortality rate as grasshoppers in presence of non-manipulated spiders. More recently, Zanette et al. (2011) showed that predator playback could decrease by 40% the number of offspring in a free living population of song sparrows (*Melospiza melodia*). Non-consumptive effect of predation can thus alter prey demography. Currently, predation is increasingly recognized as a factor which may affect prey demography via both its consumptive and non-consumptive effects (Creel & Christianson 2008). Note that non-consumptive-effect is also referred as “risk effect” (Creel & Christianson 2008), “non-lethal effect” (e.g. Pangle et al. 2007) “sub-lethal effect” (e.g. Preisser 2009; Sheriff et al. 2011b), “trait-mediated interaction” (e.g. Peacor & Werner 2001; Preisser et al. 2005) or “fear-driven effect” (e.g. Orrock et al. 2012). In the present document I arbitrarily decided to use non-consumptive effects for its non-equivocal meaning. The following section presents some main consequences of the non-consumptive effects of

predation on deer behavior and physiology and how they may affect deer population abundance.

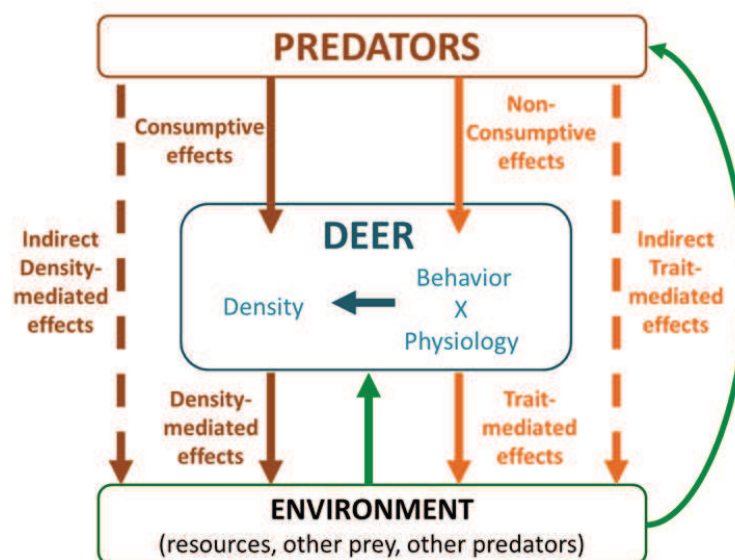


Figure 2: Conceptual representation of the effect of predation on deer and their environment (i.e. any resources and any other prey, predators or species with which deer and/or its predator may interact). Solid lines mark direct interactions and dashed lines mark indirect interactions. By its consumptive effect, predation decreases deer density and hence mitigates deer impact on its environment (density-mediated effects). By its non-consumptive effects, predation affects deer behavior and/or physiology which in turn alter deer impact on their environment (trait-mediated effects). Changes in the surrounding environment may affect deer behavior, physiology and/or density as well as predator characteristics (green-arrows). Behavioral and physiological adjustments may interact (sign “x”) and may also affect deer population density (blue arrow, but see Box 2). Note that density-dependent behavior (e.g. aggressiveness) simply due to enhanced proximity has been reported for some territorial and altricial species (e.g. carnivores, rodents: Wolff 1997), however, to my knowledge this has not been recorded for deer and hence is not considered here.

BOX 2: EFFECTS OF RESOURCES, PREDATION AND ENVIRONMENTAL CHARACTERISTICS ON DEER BEHAVIOR AND PHYSIOLOGICAL STATE AND HOW THEY IMPACT DEER POPULATION DEMOGRAPHY

The level of resources available (green) affects deer decision-making. In particular abundance, composition, distribution and configuration (easy or difficult access) of forage availability affect deer foraging behavior. The time and energy needed for food detection, handling, consumption and digestion should be considered in the overall time/energy balance achieved by deer. In addition, food quantity

and quality (nutrient and energy content) also affect deer nutrition (i.e. energy and nutrient balance between supply and physiological requirements). Predation (brown), by its consumptive effects, affects directly deer survival probability. In addition, by its non-consumptive effects, predation risks also affect deer investment in anti-predation behavior.

BOX 2 (continued)

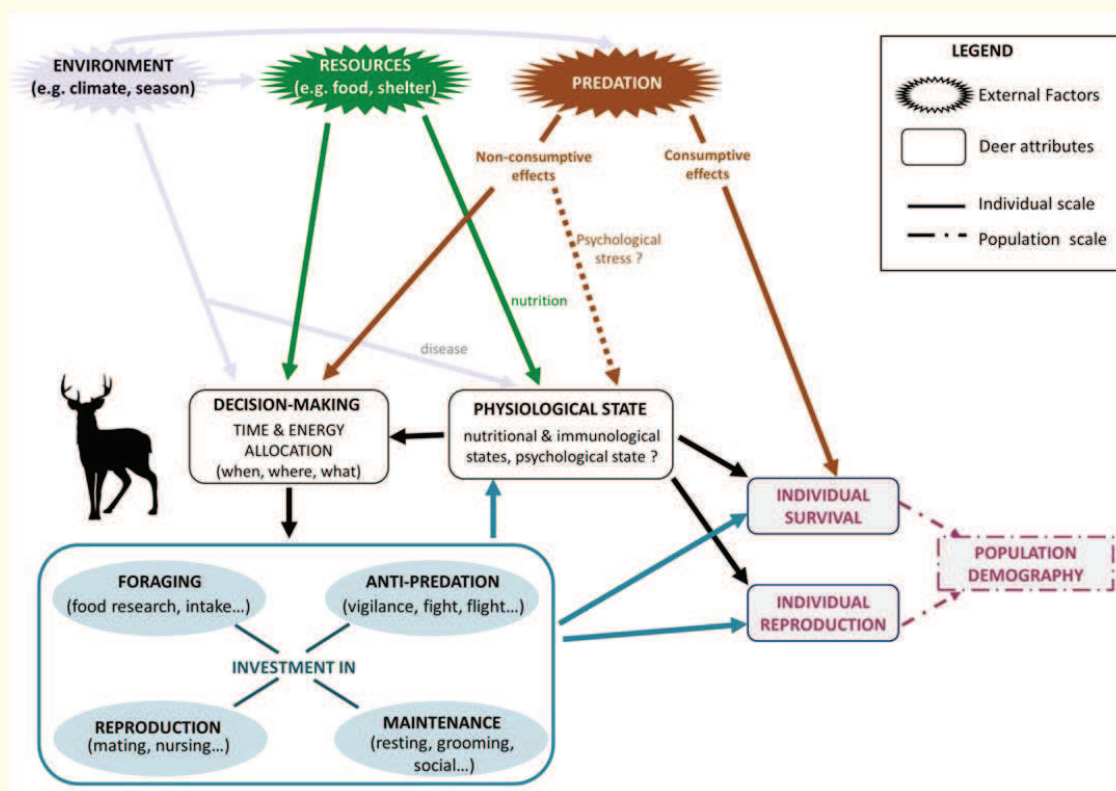


Figure B2: Effects of resources, predation and environmental characteristics on deer behavior and physiological state and how they impact deer population demography (adapted from Lima & Dill 1990; Frid & Dill 2002; Creel & Christianson 2008)

A given individual integrates information on both resources (gain) and predation risks with regard to its own state when deciding how to allocate its time and energy to perform the activities it has to achieve in its lifetime. This choice will affect the individual's physiological state which in turn will be integrated in the future decision-making and may result in further adjustments in deer behavior. Both physiological state and behavioral choices affect the individual survival and reproduction probability, which in turn translates at the scale of the population.

Environmental characteristics (grey), like weather or visibility, may alter deer perception of gain and risk and hence interfere with information integration and decision-making. In addition, environmental characteristics, like disease, also affect directly deer

physiological state and then are taken into account within the decision-making process. Finally, climate and environmental changes may also affect food quantity and quality, as well as predator motivation, efficiency and density. This may affect the overall behavioral and physiological state of deer, and hence the individual's survival and reproduction probability which finally may translate at the population level.

These factors (resources, predation and environment) could also cause a psychological stress (fear), which would directly affect deer physiological state. However, this still needs to be shown for ungulates (Clinchy et al. 2013).

II.C.2. NON-CONSUMPTIVE EFFECTS OF PREDATION ON DEER BEHAVIOR

II.C.2.a. Cost of non-consumptive effects of predation and the concept of trade-off

Predation risk may be divided into three components: the probability to encounter a predator, the probability of surviving an encounter and the time spent exposed to predation risk (Lima & Dill 1990). All of these components may be manipulated by both the prey and the predator. The interaction prey-predator may thus be understood as a game where the outcome depends on the respective ability of the prey and the predator to avoid to be killed or to kill in relation to their respective physiological and nutritional states and to their environment (Lima & Dill 1990; Lima 1998a, 2002; Caro 2005; Sih 2005). In particular, prey can adopt various anti-predation behaviors to limit their exposure to predation (see some examples below, and for a detailed review see Caro 2005). However these strategies bare costs (costs of non-consumption effects of predation) and have to be traded (Lima & Dill 1990; Lima 1998a).

A trade-off occurs when a limited resource is used for two or more incompatible features. Basically, it may be considered as an economic balance between costs and benefits of different features competing for the same resource. The optimal decision should maximize benefits while minimizing costs. Regarding anti-predation behaviors, the resource (or “currency” for the analogy with the economic balance) is mostly time (possibly energy) and the features competing are the set of possible behaviors (e.g. reproduction, foraging, resting, anti-predation: Box 2) (review in Lima & Dill 1990; Lima 1998a, 1998b).

II.C.2.b. Foraging under predation risk and decision-making

Because prey have to eat while avoiding being eaten, the trade-off between foraging and anti-predation behavior is a key component to understand prey and predator population dynamics (Lima 1998b; Schmitz 2005). Therefore, a large body of science has focused on this trade-off via both modeling (e.g. Sih 1980; McNamara & Houston 1992; Spalinger & Hobbs 1992; Houston et al. 1993; Illius & Fitzgibbon 1994; Brown et al. 1999; Lima & Bednekoff 1999; Brown & Kotler 2004; Sirot & Pays 2011) and experimental approaches (e.g. in deer: Whittington & Chamove 1995; Berger et al. 2001; Altendorf et al. 2001; Fortin et al. 2004; Stankowich & Coss 2005;

Benhaïem et al. 2008; Carrasco & Blumstein 2011). Most results may be synthesized in the conceptual framework proposed by Lima & Dill (1990) which addresses the concept of decision-making under predation risk. In the present document, I focus on the trade-off between foraging and anti-predation behaviors, but note that Lima & Dill's framework (1990) remains relevant for any kind of trade-off involving predation risk.

In a nutshell, decision-making under predation risks is a balance between benefits of anti-predation behaviors (i.e. benefits of future opportunities enabling the surviving individual to reproduce) and the cost of lost opportunities (i.e. benefits of alternative activities that are lost if not done) in relation to the levels of risk present. This is thus simply a balance between the fitness consequence of surviving (benefits of anti-predation behavior) and the fitness consequence of the other activities, such as energy gained by foraging (costs of anti-predation behavior). Here, fitness refers to the ability of an individual to survive and reproduce in its environment (Lima 1998a).

This balance may be split in three components: the level of risk, the level of gain and the prey individual state (i.e. physiological and nutritional state). All other things being equal, the theory predicts that: (i) if risk decreases prey should invest less time in anti-predation behavior because the probability to be killed decreases and lower levels of anti-predation behavior are thus needed to maintain a similar chance to survive; (ii) if gain decreases prey should invest more time in anti-predation behavior due to a decrease in the cost of lost opportunities. Say differently, in presence of lower levels of gain prey should tolerate lower levels of risk; (iii) if prey state decreases prey should invest less time in anti-predation behavior because the future opportunities to survive and reproduce are lower which reduces the benefits of anti-predation behavior. Individuals with lower energy state (e.g. starved) should tolerate higher level of risks because they have lower future fitness (i.e. future opportunity to reproduce) and hence less gains (Lima & Dill 1990). Note that it may be understood simply as an assessment of the marginal value of gain for the prey fitness, defined as the relative gain of fitness obtained in investing a given amount of resources (e.g. time) in anti-predation behavior when compared to the gain of fitness obtained when investing the same amount of resource in other behaviors (Lima 1998a; Brown 1999).

II.C.2.c. Risk perception: the foundation of risk management

Within this framework, prey individuals manage risk through a decision-making based on their individual evaluation of the levels of risk and gain as function of their state. Individuals decide what to do according to their *perception* of risk and gain in relation to their state (Lima 1998a, 1998b; Lima & Steury 2005). Behavioral response to predation risk is a particular kind of information treatment and involves three steps: 1) information acquisition (i.e. stimulus filtering) ; 2) information processing (i.e. risk or gain assessment); and 3) decision-making *per se* (Blumstein & Bouskila 1996; Lima & Steury 2005).

Information acquisition (step 1) depends on both the cues available and the individual's sensory mode of detecting cues. This results generally in a filtering of the available information (Blumstein & Bouskila 1996; Lima & Steury 2005). Acquired information is then processed via the cognitive system to assess the level of risk or gain, namely the *perceived* risk or gain (sensu Lima & Steury 2005) (step 2). This information assessment integrates both acquired information and the individual characteristics (e.g. inherited traits, previous experience). *Perceived* risk and *perceived* gain are then coupled and traded as function of the individual state during the decision-making process. This produces the observed behavioral response (step 3).

Consequently, in the process of risk management one may identify three kinds of risk (or gain): the *actual* risk (prior to the step 1), the *perceived* risk (at the end of the step 2) and the "*observable*" risk (at the end of step 3). Because by studying animal behavior we measure only the "*observable*" risk, it is important to consider these differences when interpreting how individuals respond to risk (Blumstein & Bouskila 1996; Lima & Steury 2005). In particular, one should keep in mind that the "*actual*" risk may not be the one "*perceived*" by the individual and that an absence of behavioral response does not necessarily account for an absence of risk perception. Indeed, individuals may perceive risk but may not be able to respond (e.g. phenotypic constraints: Relyea 2005) or estimate they should not respond due to physiological or environmental constraints (e.g. Gill et al. 2001; Lima & Steury 2005; Relyea 2005). This emphasizes the critical role of the "*context*" (e.g. environment, prey state) in which information is acquired and in which the decision-making takes place.

Finally, one may also reconsider the relative importance of the prey background (e.g. previous exposure to risk) as function of the kind of anti-predation behavior studied. A behavior can be learnt or innate. A learnt behavior results from enduring changes in its underlying mechanism as function of experiences with environmental events (Thorpes 1956; Griffin et al. 2000). Generally a learnt-behavior results from a process of trials and errors (Thorpes 1956) and may involve a single or a few trials with direct or indirect exposure to a predator (Griffin et al. 2000; Brown & Chivers 2005). By definition, one expects such learnt behaviors to be lost if not expressed during a generation. To the contrary, an innate or “hard-wired” behavior is expected to be functional at the first encounter with a predator (Blumstein 2002). The persistence of an innate trait depends on the selection pressure exerted on it (Lahti et al. 2009). Given the kind of behavior considered, the importance of prey background may thus be more or less important in the assessment of risk. However, innate behaviors may be improved with time and subsequent experience (Blumstein 2002), whereas learnt behavior may be genetically predisposed (e.g. Griffin et al. 2002). Anti-predation behavior could thus be understood as the results of the interaction between inherited traits and ontogenic experiences (Curio 1993). In both cases prey-background is thus likely to play a critical role in decision-making, and has to be considered.

Prey individuals are thus dynamic agents which assess and manage the risk in adjusting their behavior. Strategies used by animals in relation to the trade-off between foraging and anti-predation behaviors have been studied in many taxa including invertebrates (e.g. Peckarsky et al. 1993; Schmitz et al. 1997; Hopper 2001; Denno et al. 2005; Pangle et al. 2007) and vertebrates (e.g. in fish: Godin & Smith 1988; Grand & Dill 1999; e.g. in reptiles Downes 2001; Cooper 2008; in amphibians: Buskirk et al. 2002; Martín et al. 2006; e.g. in birds Lima 1985; Bednekoff & Lima 2005; in mammals: Blanchard & Fritz 2007; Kotler et al. 2010; but see Caro 2005 for a review). In the following section I present a few examples of the trade-off between foraging and anti-predation behaviors reported for deer. For further examples and details on anti-predation strategies used by deer see Geist (1981), Hatter (1982) and Caro (2005).

II.C.2.d. Risk management in deer: some examples

Spatio-temporal management: where, when and what?

“Where and when to go? “: a question of habitat selection

As highlighted by Geist (1981) “the best way to avoid predator is to go where there are none”. Avoiding risky area is a very common strategy among animals which enable them to reduce their probability to encounter a predator (Lima & Zollner 1996; Sih 2005). In particular, deer are known to manage risk at various spatio-temporal scales: i) deer may manage risk locally at the scale of the day. For example roe deer (Bonnot et al. 2013) and white-tailed deer (Kilpatrick & Lima 1999) avoid hunting areas by day (hunting period) but use them by night (non-hunting period); ii) deer may decide to avoid completely some risky places at the scale of the period of risk. For example, white-tailed deer avoid roads during the hunting season (Kilgo et al. 1998); and iii) deer may decide to leave the risky area completely at the scale of the seasons. For example, populations of black tailed deer (McNay 1995) or elk (Hebblewhite & Merrill 2007) undertake annual migrations covering distances ranging from 6 to 70 km to avoid natural predators and reach lower risk areas. In addition, deer may also limit their chance to be attacked by selecting habitats which improve their probability to escape if attacked (Caro 2005). This was observed in mule deer which stay close to steep slopes, river banks and cover in winter, places where deer can more easily outdistance and outmaneuver a predator (Geist 1981; Lingle & Wilson 2001).

However, habitats may present different levels of gains (i.e. food quantity and quality in forest vs. crop area for roe deer: Bonnot et al. 2013) associated with different levels of risk (e.g. risky crop field where hunting occurs vs. safe forest area where no hunt occurs). Habitats may also differ in the way they affect the probability for a deer to encounter and/or to be killed by a predator (Hebblewhite et al. 2005). Deer may thus not be able to avoid risk completely and hence are likely to have to manage their exposure to risk in managing their activities and in particular the time they devote to anti-predation behaviors, like vigilance.

“What to do?”: time allocation to vigilance

Vigilance is an anti-predation behavior shared by most taxa (Caro 2005) which may be understood in its broader sense as the visual awareness of an individual to its environment. The

underlying idea is that the early detection of predators may reduce the probability of an individual to be killed by giving more time to the individual to cope with the situation (e.g. deterring the predator (Box 3), fleeing or being prepared to flight) (e.g. Lingle & Wilson 2001; Lingle & Pellis 2002; review in Caro 2005).

In practice many definitions have been used to identify vigilance behavior in animals and present various degrees of incompatibility between foraging and anti-predation behavior (e.g. including or not chewing bouts: Fortin et al. 2004; including or not food intake: Bednekoff & Lima 2005, review in 1998b; Caro 2005). Vigilance is thus expected to be more or less costly according to the definition considered. In particular, the possibility to combine vigilance with food handling (e.g. chewing bouts) was estimated to reduce by 15% the vigilance cost (Fortin et al. 2004). In this study the vigilance cost was estimated as the reduction in bite rate caused by vigilance. This reduction was mitigated when vigilance occurred during chewing bouts. Nevertheless, vigilance remained costly (total reduction of 26% in elk bite rate) and was tentatively explained by a possible mismatch in the duration of chewing bouts and vigilance bouts or by physical constraints on food processing. In addition, although animal may pay attention to their environment while feeding (Bednekoff & Lima 2005) exclusive vigilance behavior (more costly) seems to be more efficient and remains an important component in the trade-off faced by foraging individual.

Furthermore, a brief review of vigilance studies in deer highlighted the importance to consider : (i) prey characteristics, such as sex, age or reproductive status (e.g. Laundré et al. 2001; Lung & Childress 2007; Reimers et al. 2011); (ii) prey social context, including the size and the composition of the group (e.g. presence of young) as well as the position of the focal individual in the group (e.g. Molvar & Bowyer 1994; Sieber 1995; Liley & Creel 2007); (iii) predator characteristics, such as hunting strategies (e.g. stalker or hunter), predator motivations and predator group size (e.g. Bednekoff & Lima 2002; Liley & Creel 2007; review in Lima 2002); and (iv) environmental factors such as daylight, snow cover or visibility (e.g. Beauchamp 2007; Liley & Creel 2007; Sirot & Pays 2011) (but see Elgar 1989; Quenette 1990; Bednekoff & Lima 1998b; Caro 2005; Mitchell 2009 for reviews). All these features should be integrated when interpreting changes in vigilance levels. For instance, white-tailed deer in Ossabaw Island, Georgia, US, seem

less vigilant in open pastures than in wooded pastures where visibility is reduced and where ambushed-attacks by wolves or cougars are less easily detectable (Lagory 1986). On the contrary, roe deer in France are less vigilant in closed forests than in open areas where hunting occurs (Benhaïem et al. 2008).

Vigilance studies inform us on how individuals allocate their time within a given patch, whereas studies on habitat selection inform us on how individuals allocate their time among patches (i.e. the time spent in a patch). Because, individuals may manage both at the same time, Brown (1988, 1992, 1999) developed an index integrating both spatial scales, referred as the giving up density (GUD).

“Where, when and what?”: GUD an integrative index

The giving-up density (GUD) measures the density of food left by an individual when leaving a given patch of food and may be understood as a “behavioral titration of risk” (Brown & Kotler 2004). The underlying idea of GUD is that, all other things being equal, the more vigilant an individual is or the less time an animal spends in a given patch and the more food it will leave behind when deciding to abandon the patch (higher GUD). Because the time spent vigilant and the time spent in a patch may change simultaneously, GUD provide an integrated behavioral response of individuals to risks (Brown 1999; Brown & Kotler 2004).

Altendorf et al. (2001) used GUD and vigilance measures to study how mule deer perceive and manage risk between different forest habitats. They show that mule deer manage predation risks at both the habitat and the microhabitat scales. They highlight that in Douglas fir forest (riskier habitat), deer seem to perceive more risk (higher GUD) in the forest interior than at the forest edge, whereas vigilance levels were higher at the forest edge than in the forest interior. Mule deer spent thus less time in the forest interior but when they were present they focused on foraging. On the contrary, in the mountain mahogany forest (safer habitat), deer used as much the forest edge as the forest interior (similar GUD). These contrasting results demonstrate that deer perceive and manage risk at different spatial scales.

What do deer do when a predator is detected?

When a predator is detected a prey individual can either remain or escape (flight). This decision is context-dependent and results from an assessment of the risks of captures (e.g. distance to the predator, predator motivation, habitat), the costs of flight (e.g. energy cost, habitat) and the alternative options (e.g. presence of a refuge) (Ydenberg & Dill 1986). If the individual stays despite the risk assessed it can either keep foraging, or try to avoid detection (e.g. staying hidden in good cover: Dasmann & Taber 1956) or try to deter the attack (Box 3). However if the predator maintains its approach, the individual has to decide at which point it should flee according to the context (see above). This trade-off has been commonly measured via flight initiation distances, the distance at which a prey runs away at the approach of an intruder (Ydenberg & Dill 1986). Flight initiation distance is also referred to as “flight distance”, “flush distance”, “escape distance”, “reaction distance” or “approach distance” (Stankowich & Blumstein 2005; Tarlow & Blumstein 2007; Stankowich 2008). I arbitrarily chose to use “flight distance”. Accordingly to Lima & Dill (1990), flight distance is expected to be shorter in safer areas (i.e. less investment in anti-predation behavior with reduced risk, Case (i)), to be longer in presence of low quality food (i.e. low gain – Case (ii)) and to be shorter for prey which are in poorer condition (Case iii).

This was mostly validated by field studies on birds (Lima 1985; Stauss et al. 2005; Eason et al. 2006; review in: Stankowich & Blumstein 2005) and mammals including deer (e.g. Dill & Houtman 1989; Lagos et al. 2009; review in: Stankowich & Blumstein 2005; Stankowich 2008). For example, black-tailed deer flees at greater distance and takes its decision quicker (i.e. delay between the detection of the intruder and the flight) when it is approached directly or at higher speed which are perceived as riskier situations (Stankowich & Coss 2005). In addition, Stankowich & Coss (2005, 2007) also demonstrate that sex and habitat can alter flight distance behavior, supporting the fact that decision-making integrates both individual and environmental factors.

Interestingly, at the approach of a predator deer may also opt for “fight” rather than for “flight” (Lingle & Pellis 2002). For example under similar conditions, although white-tailed deer are

more eager to run away an approaching coyote, mule deer are more eager to stay and bundle in larger groups to face the predator (Lingle & Pellis 2002). This highlights another anti-predation strategy commonly found in animals: being in group or as the famous adage says “union makes strength” (Lima 1995; Caro 2005).

BOX 3: PURSUIT DETERRENCE SIGNALS IN DEER

When a prey has detected a predator, it can rely on pursuit deterrence signals to warn the predator that it has been detected and has lost the surprise effect (Caro 1995). Generally, pursuit deterrence signals are honest signals of prey’s quality and may thus be understood by the predator as a piece of evidence that pursuing the attack would be a waste of time and energy for both of them since the prey is likely to escape (Caro 2005). Although the concept is appealing, identifying pursuit deterrence signals is not easy because it requires : i) to observe the interaction prey - predators; and ii) to demonstrate that the prey manage to convince the predator to give up via a single or several signals while controlling for other confounding factors (e.g. prey and predator states and motivations, cover, topography) (Caro 1994, 1995, 2005). Therefore, usually pursuit deterrence signals have been identified in eliminating competing hypotheses

rather than by being directly tested. For example, it has been suggested that white-tailed deer snorting may notice to the predator that it has been detected whereas costly gaits like stotting or “alarm walk” in black-tailed deer may inform on the speed and the ability of deer to escape and attack (Caro 1994; Stankowich & Coss 2008). Tail-flagging in white-tailed deer may also be a pursuit deterrence signal (Caro et al. 1995). Indeed flagging individuals have been reported to flee at greater speeds than non-flagging individual. Flagging may thus be a honest signal informing on prey’s ability to escape. However, dropping the tail may also confuse the predator during the chase, what may help in making deer inconspicuous (Caro et al. 1995). Both explanations are not exclusive and highlight the possible multifunction of different signals as well as the difficulty in identifying pursuit deterrence signals

Being in group: a trade-off for safety.

Being in group as anti-predation behavior is a whole theme of research in itself (e.g. Lima 1995; Grand & Dill 1999; Beauchamp 2001, 2003; Hebblewhite & Pletscher 2002; Bednekoff 2003; Bednekoff & Lima 2004; Fernández-Juricic et al. 2004; Caro 2005; Martín et al. 2006; Ale & Brown 2007; Sirot & Touzalin 2009). In particular many studies have investigated the respective

benefits and costs of being in a group when facing predation risk. I briefly present the main results but see Caro (2005) for a detailed review.

Grouping may present several advantages to manage risk. First, it may enhance the probability to detect a predator. Indeed, individuals in a group have access to public information from both the environment (e.g. predator cue, visibility) and from other group members (e.g. behavioral response). Depending on the rate of information transmission among group members, individuals may have access to a larger set of cues promoting earlier detection (e.g. Pulliam 1973; Bednekoff 2003; Fernández-Juricic et al. 2004; Sirot & Touzalin 2009). Secondly, grouping may limit the risk to be captured. Indeed because a predator may target a single individual per attack, then the more individuals there are in group and the less chance to be attack there is (“dilution effect”: Hamilton 1971). However, this is likely to interact with the predator behavior (e.g. hunting mode and target identification) and the level of synchrony in the response of group members to the presence of a predator (but see Bednekoff & Lima 1998a). Note that simultaneous flight response may also confuse the predator during the attack reducing thus the probability of the prey individual to be killed (Caro 2005). Finally, animals in groups are more eager to intimidate a predator or counter-attack, as observed in mule deer (Lingle 2001).

However, although grouping may be advantageous, it may also bare costs. For example, larger groups may be more easily detected than smaller groups. This was reported for elk for which herds > 6 animals were significantly more detected by wolves than herds < 5 animal in Banff National Park, Canada (Hebblewhite & Pletscher 2002). Similarly, grouping may also increase competition for resources (e.g. food), as observed in sika deer at salt licks (Ping et al. 2011) or in moose that present reduced foraging efficiency in larger groups (Molvar & Bowyer 1994). Thus, again, grouping as any anti-predation behaviors presents benefits and costs, and is one possible response among the set of possible behaviors available to prey to manage predation risk.

This short description of some anti-predation behaviors aims at highlighting the inherent trade-off involved in any behavioral response to predation risk. It also pinpoints the importance of the “context” (e.g. habitat, predator behavior, presence of neighboring prey) and how it may interact in the evaluation of cost and benefits. Another key component in risk management is

whether the risk is permanent or temporary. The importance of the temporal regime of risk in animal anti-predation behavior has been explicitly stated by Lima & Bednekoff (1999) and named the “risk allocation hypothesis”.

Risk Allocation Hypothesis

The risk allocation hypothesis considers an environment where predation risk is highly variable in space and time. The underlying idea is that time is limiting and prey have to reach a minimum level of energy to survive. Thus, under frequent and long periods of high predation risk, prey cannot spend their whole time being vigilant and should reduce their investment in vigilance in favor of foraging. As a consequence, Lima & Bednekoff’s (1999) model predicts that in situations when periods of low-risk level are long and period of high-risk level (pulse of risk) are rare prey should invest more in anti-predation behaviors (e.g. vigilance) in presence of risk than in situations when period of high-risk level are long and the period of low-risk level are rare (pulse of safety). Indeed, when risk is rare (pulse of risk), prey will have other opportunities in the future to resume feeding and hence can invest time in non-foraging behavior during high-risk periods. On the contrary, when risk is frequent, prey won’t have a lot of other opportunities to eat and the cost of lost opportunities is too high to invest a lot of time in anti-predation behavior. Thus, anti-predation investment should be higher during rare and short pulse of risk than during frequent and long period of risk.

Although appealing, validating the risk allocation hypothesis completely has proven difficult, in particular because lower response to risk in frequent and long period of risk may also account for an increasing tolerance of the individual to risk (review in introduction: Rodriguez-Prieto et al. 2009). For example, accordingly to the risk allocation hypothesis, Creel et al. (2008) show that in the Yellowstone National Park, Wyoming, U.S., elk are more vigilant when exposed to short and rare presence of wolves than when exposed to long and frequent presence of wolves. However, elk exposed to long risky periods are also overall less vigilant than elk in safer areas, which could be interpreted as a higher tolerance of elk to wolves in areas where wolves are more frequent. Whether different investment in anti-predation behaviors are due to different

temporal risk pattern (risk allocation hypothesis) or to different risk perception (tolerance) or to their interaction may still need to be investigated (Rodriguez-Prieto et al. 2009).

Interestingly, this study highlights the remarkable ability of deer to adjust their behavior to risk levels including different temporal regimes of risk. Because deer, and prey in general, respond to risk in changing their behavior, and that such changes are likely to affect their interaction with their environment (Figure 2), a new avenue of research has focused on how risk could affect the ecosystem composition and functioning, namely the ecology of fear (Brown et al. 1999).

II.C.2.e. Ecology of fear: a new hope for managing abundant deer populations?

As presented previously, deer manage risk via various strategies, including, among others, changes in their habitat use (e.g. avoiding area) and in their foraging activity (e.g. vigilance). Because deer can have major impacts on their environment (see I) changes in deer behavior and/or physiology is likely to translate at the plant level, called cascading effects (Figure 2). Note that as discussed below (see I) “cascading effects” are not necessarily linear effects and actually may affect any life-beings interacting with deer. This suggests that by managing risk one can manage deer behavior and hence possibly their impact on their environment. This exciting perspective has raised a great interest in scientists and managers and seemed supported by the classic example of the reintroduction of wolves on elk behavior in Yellowstone National Park (Laundré et al. 2001; Ripple & Beschta 2006). There, following the return of wolves, elk became more vigilant (Laundré et al. 2001; Liley & Creel 2007) and avoided some areas where stands of aspen (*Populus tremuloides*), a plant species that suffered from heavy browsing pressure previously, could regenerate (Fortin et al. 2005; Beschta & Ripple 2007; but see Middleton et al. 2013 for a synthetic review). This success story was put forward to promote the possibility to mitigate deer impact on some plants, at least locally, via a “landscape of fear”.

However, mechanisms at the origin of such a landscape are still debated (Middleton et al. 2013), and more generally many unknowns remain in the possibility to manage deer, or abundant large herbivore populations, via non-consumptive effects of predation. Among others, mechanisms

involved in risk perception in wild animals are rarely known (Lima & Steury 2005; Clinchy et al. 2013) and understanding how non-consumptive effects translate at the population scale (i.e. how they affect prey survival and reproduction) is still in its early stage, especially in large herbivores (Creel 2011; review in Clinchy et al. 2013; Zanette et al. 2013).

Indeed, although the effect of wolf-induced risk on elk behavior in Yellowstone National Park is one of the most cited example of the ecological effects of predator-prey interactions, results remain ambiguous (Middleton et al. 2013). On the one hand, in presence of wolves, elk have modified their diet (Christianson & Creel 2008), have reduced their energy intake (Christianson & Creel 2010) and elk females have produced less calves (Creel et al. 2007; Creel & Christianson 2008), suggesting that wolves affect both elk survival (malnutrition) and reproduction. On the other hand, White et al. (2008, 2011) did not find a strong effect of wolves on elk winter diet or on elk female body conditions or on their pregnancy rate (but see Middleton et al. 2013a for a review). These discrepancies highlight the difficulty to assess non-consumptive effects of predation which in addition may not necessarily be permanent. In the Yellowstone case study, the debate on the relative importance of consumptive vs. non-consumptive effects of wolf predation on elk population dynamics is ongoing and echoes the current dilemma faced by managers : “to kill or to scare”. Further studies are thus required to better assess if risk management may be a solution to manage deer and if yes, under which circumstances (Creel 2011; Crowsigt et al. 2013).

Interestingly, this section on anti-predation behavior shows how much behavior and physiology are intertwined: on the one hand, prey individual state (i.e. physiological state) participates in the decision-making process and hence affects prey investment in anti-predation behavior. On the other hand, anti-predation behaviors affect how a prey uses its resources. This affects its nutritional state and hence its physiological state. This interaction is at the foundation of a possible management of abundant large herbivore population by risk. In addition, although not accepted by the whole scientific community yet, psychological stress (fear *per se* sensu Creel et al. 2009) could also affect individual physiology directly (Clinchy et al. 2013). Thus, either indirectly (behavior-mediated) or directly (fear) predation risk may have physiological

consequences. The following section investigate how predation risk may affect individual physiological state and provide a brief state of art on our current knowledge on deer physiological response to risk.

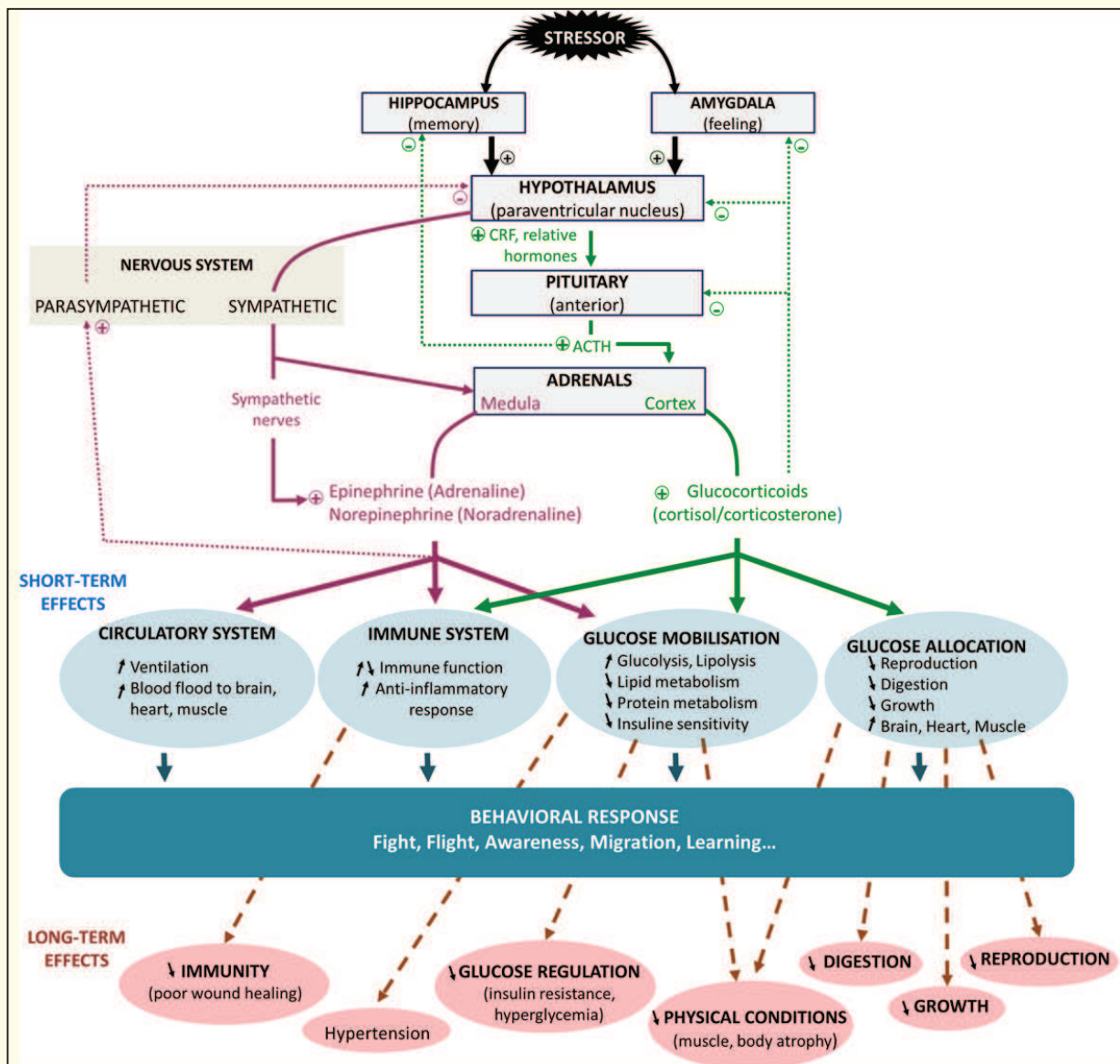
II.C.3. NON-CONSUMPTIVE EFFECTS OF PREDATION ON DEER PHYSIOLOGY

II.C.3.a. Physiological trade-off

Similarly to the behavioral response of a prey individual to predation, physiological responses may be understood as trade-off (Lima 1998a; Möller et al. 1998; Millspaugh et al. 2001; Pereira et al. 2006). In the physiological trade-off the resource traded is mostly energy (possibly nutrients) and the activities in competition are reproduction, growth and homeostasis (i.e. maintenance of physiological constants (e.g. temperature, pH) necessary for animal survival: Robbins 1993).

A stress is a state in which homeostasis is lost and stressors are any events or factors causing stress (Reeder & Kramer 2005). Stressors may be physiological (e.g. starvation due to predation risks) or psychological (e.g. fear) (Wingfield 2003; Reeder & Kramer 2005; Clinchy et al. 2013). To neutralize the effect of a stressor and to limit the deleterious impacts of an impaired homeostasis, a cascade of physiological events occurs in order to reestablish the internal equilibrium via behavioral (e.g. flight in front of a danger) and physiological changes (Box 4). This cascade is referred to the stress response (Reeder & Kramer 2005). By definition, stress response is energetically costly to produce and involves an energy re-allocation among physiological activities (reproduction, growth, and homeostasis). This may alter the individual survival and/or reproduction success (e.g. chronic stress, Box 4) and hence may translate on the population dynamic level (Lima 1998a).

BOX 4 : PHYSIOLOGICAL IMPACTS OF A STRESSOR (adapted from Möller et al. 1998; Boonstra et al. 1998; Sapolsky et al. 2000; Reeder & Kramer 2005; Wingfield 2005; Romero & Butler 2007; Sheriff et al. 2011)



Stress response mechanism

A stressor (or emergency) is detected by the amygdala and/or the hippocampus in the brain which sends neuronal signals to activate the hypothalamus. The hypothalamus initiates then the stress response via two pathways:

1. The sympathetic nervous system (purple pathway) operates within a few seconds and lasts a few minutes. The hypothalamus stimulates the release of catecholamine hormones (i.e. epinephrine (adrenaline) and norepinephrine (noradrenaline)) in the blood by activating the adrenal medulla via the sympathetic nervous system. Some peripheral sympathetic nerves also contribute to the release of norepinephrine in the blood.

BOX 4 (continued)

This release of adrenaline and noradrenaline affects the circulatory system by increasing heart rate, ventilation and blood flow to the brain, heart and muscles among others. It also promotes glucose release in the blood and wound healing. These quasi-immediate changes help mobilize energy in order to face an acute threat and hence were often called the “fight or flight response” (Wingfield et al. 1998; Möller et al. 1998).

2. In the meantime, the hypothalamic-pituitary-adrenal axis (HPA axis - green pathway) is also activated. The hypothalamus releases corticotropin-releasing factor (CRF, previously referred as CRH for corticotropin-releasing hormone) and related hormones which stimulate the release of adrenocorticotropic hormone (ACTH) into the blood by the anterior pituitary. ACTH travels to the adrenal cortex and stimulates the release of glucocorticoids (corticosterone and/or cortisol according to the species) into the blood. Glucocorticoids reach then different target cells where they activate receptors stimulating or inhibiting the synthesis of proteins altering the cell and hence the target organ's function. Changes in protein synthesis are time consuming. Although glucocorticoids reach a peak in the blood within 3-5 minutes, their effects take place only after 20-30 minutes and may last hours to weeks or longer according to the situation. Glucocorticoids have a wide range of target-cells and overall aim at maintaining a high-level of glycaemia. This involves (i) changes in nutrient metabolism in favor of glucose release [e.g. reducing lipo- and proteogenesis (lipid and protein synthesis) and stimulating lipo- and proteolysis (lipid and protein catabolism to produce glucose)], (ii) changes in glucose allocation in favor of the brain, heart and muscles and to the detriment of other organs involved in reproduction, digestion and growth; and (iii) changes in immune functions, which may be promoted in the very short term but are then inhibited, possibly to avoid auto-immune reactions. Similarly to the sympathetic nervous pathway, these changes provide energy for activities essential in presence of a stressor (e.g. movement, awareness)

to the detriment of others (e.g. reproduction, growth).

Stress response regulation and chronic stress

Stress response occurs when these pathways are activated above basal levels and ends when physiological parameters are back to their baseline (Reeder & Kramer 2005). In absence of stressor, hormones, like glucocorticoids, are regulated via negative feedbacks (dashed lines) which ensure the maintenance of functional and non-deleterious hormone concentrations. A stressor disrupts momentarily this feedback and activates the HPA axis resulting in a peak of glucocorticoids. Stress response efficiency and effects (short and long-term) depend on the peak's magnitude and on the time-course needed for the feedback control to down-regulate the glucocorticoid concentrations to basal levels (Dallman & Bhatnagar 2011; review in Sheriff et al. 2011). The quicker and higher the peak is, the quicker and more acute the stress response is, because it results in a quick release of energy available for an individual to cope with a stressor. However, the longer the peak is and the higher the risk of deleterious effects. Thus, an ideal stress response would be high and brief peaks of glucocorticoids in response to stressors (review in Romero & Butler 2007; Sheriff et al. 2011).

Under punctual and acute stressor, feedback mechanism down-regulate glucocorticoid levels efficiently. Glucocorticoids return to their basal levels in less than an hour but the newly synthesized proteins remain active for longer which enables the individual to finish coping with the emergency situation. However, in presence of frequent and/or prolonged stressors (i.e. chronic stress) feedback signals are weak and less efficient in down-regulating glucocorticoids (Wingfield et al. 1998). Glucocorticoid-induced changes are thus maintained for longer periods and cause deleterious physiological dysfunction. In particular, prolonged disorders in immune, circulatory or digestive systems, as well as in physiological constants like

BOX 4 (continued)

glycaemia, are detrimental for the animal survival. In addition, prolonged reduction in the energy allocated to reproduction or growth may dramatically reduce the reproductive success of the animal. Thus, whereas short-term effects of stress response promote individual survival by enabling it to cope with an acute stressor, prolonged effects of stress response under chronic stress are adverse for the individual survival and reproduction.

Interestingly, chronic stress may alter the stress response function. First, chronic stress may alter the HPA sensitivity to a stressor. HPA sensitivity to a given stressor may be reduced and hence individuals do not perceive the stressor as a stressor anymore. No stress response is activated and glucocorticoids remain at their basal levels even in presence of the stressor. This is called “acclimation” (Romero 2004). On the contrary, HPA sensitivity to a given stressor may be enhanced. In this situation, individuals are more responsive to a stressor and mount stronger stress response to the repeated exposure to the stressor. This is called “sensitization” (Romero 2004). Finally, chronic stress may also promote the responsiveness of animal to other stressors. In this situation, in presence of a different stressor individuals mount stronger stress response than in presence of the previous stressor. This is called “facilitation”(Romero 2004). Most results were initially obtained in laboratory rats (Romero 2004) but the general conclusion may be adapted to other mammals. For instance, farmed Grevy’s zebras (*Equus grevyi*) translocated to Meru National Park exhibited higher glucocorticoid levels in this

unfamiliar area up to 11 -18 weeks after translocation. After this acclimation period, their glucocorticoid levels were back to normal (Franceschini et al. 2008). Similarly, red deer males response to an ACTH challenge was facilitated in males subject to social stress due to changes in their group composition in contrast to males in unchanged groups (Hanlon et al. 1995). These few examples highlight the range of adjustment possible in animal response to prolonged stressors.

Moreover, individuals may also become “resistant” to glucocorticoids. In this situation, they still perceive the stressor and mount a stress response with its associated high glucocorticoid levels. However, some target-cells do not respond to this increase in glucocorticoids and maintain their normal activity. For example, this was reported in some short-live rodent species in Australia which maintained normal reproduction cycle despite high glucocorticoid levels. After breeding, all animals died due to the detrimental catabolism of essential enzymes induced by glucocorticoids (Wingfield&Sapolsky 2003).

Finally, individuals may also adopt different behavioral strategies which would affect their exposure duration to a stressor and the intensity perceived by the individuals (e.g. review in Wingfield 2003, 2013). Both behavioral and physiological adjustments interact thus together to shape individual stress responses and more research is needed to better assess how free-ranging animals respond to various stress regimes (Angelier & Wingfield 2013).

II.C.3.b. Stress mediators: Catecholamine and Glucocorticoid hormones

Stress response in most vertebrate taxa involves two complementary pathways : (1) the sympathetic nervous system (Box 4) acts within a few seconds through catecholamine hormones which stimulate heart rate, breathing rate, blood flow to brain, to heart and to muscle and the release of glucose (energy source) in the blood; and (2) the hypothalamic-

pituitary-adrenal axis (HPA axis - Box 4) acts within a few minutes via glucocorticoids, steroid hormones, which help to maintain a high level of glycaemia (glucose concentration in blood) (Möller et al. 1998; Reeder & Kramer 2005; Wingfield 2005; Sheriff et al. 2011b; Box 4). Both pathways “dovetail” to mobilize and re-allocate energy to the activities assessed priority to face the stressor in both the immediate (catecholamine-induced changes) and short- to medium terms (glucocorticoid-induced changes) (Romero & Butler 2007). However, this energy is spent to the detriment of reproduction, growth and of maintenance and efficiency of the immune system. This, over the long term, can have deleterious effects on individual survival and/or reproduction (Möller et al. 1998; Reeder & Kramer 2005; Wingfield 2005; Sheriff et al. 2011b; Box 4). These long term effects may occur in presence of prolonged and/or repetitive exposure to a stressor, referred to “chronic stress” (e.g. Veissier & Boissy 2007; Wielebnowski & Watters 2007; Busch & Hayward 2009). For instance, Boonstra et al. (1998) reported that Alaskan snow hares suffering successive years of high predation pressure had higher basal levels of glucocorticoids associated with higher body mass loss over winter, lower litter size and higher immunosuppression than snow hares under lower predation risks.

The degree at which a stressor causes chronic stress and its associated deleterious consequences depends on the animal’s perception of and sensitivity to the stressor and on the context (i.e. energy available and required for other activities) (Romero 2004). Therefore, a large body of science has focused on the physiological response of animal to stress (e.g. Möller et al. 1998; Sapolsky et al. 2000; Wingfield 2003, 2005, 2013; Reeder & Kramer 2005; review in Sheriff et al. 2011b)

II.C.3.c. Physiological measurements of stress

Both pathways of stress response can be studied. The response of the sympathetic nervous system to a stressor cannot be assessed directly via the levels of catecholamines due to their too short lifespan (half-life: 10-30s: von Holst 1998). However, it can be studied via changes in heart or breath rates (e.g. Moen 1978; Chabot et al. 1996; Reeder & Kramer 2005). To the contrary, glucocorticoids have a longer life span and may be used to study the response of the HPA axis to a stressor. Glucocorticoids have been the focus of many studies on animal stress

(e.g. review in Sapolsky et al. 2000; Romero 2004; Boonstra 2005; Busch & Hayward 2009; Sheriff et al. 2011b). For example, increasing glucocorticoid levels have been reported in white-tailed deer which body mass decreased due to winter starvation (Delgiudice et al. 1990). Similarly, mule deer fawn presented higher glucocorticoid levels in high-density populations with reduced food supply than in lower density populations with larger food supply (Saltz & White 1991). Higher glucocorticoid levels were furthermore correlated to higher mortality rates due to starvation in fawns in high-density populations (Saltz et al. 1992). Social status may also affect glucocorticoid levels in mammals (e.g. van Schaik et al. 1991; Creel 2001). For example, Bartoš et al. (2010) reported that changes in the social structure of groups of red deer males affected their basal levels of glucocorticoids. However, no significant differences in basal glucocorticoid levels were observed between dominant and subordinate pudu (Bartos et al. 1998) or Pere David's deer males (Chunwang et al. 2004).

Glucocorticoids levels may be quantified either in plasma (e.g. Morton et al. 1995; Romero 2002), in saliva (e.g. Millspaugh et al. 2002) and in hair (e.g. Ashley et al. 2011) or as metabolites (components issue from molecule degradation) in urine (e.g. Saltz & Cook 1993) or in feces (e.g. Dehnhard et al. 2001; Millspaugh et al. 2001). The temporal scale at which stress levels are integrated varies with the sample considered. From the shorter to the longer temporal scale, plasmatic concentrations inform on instantaneous levels of glucocorticoids, salivary concentrations on the hourly to daily levels of glucocorticoids, fecal concentrations on the average daily to weekly level, and hair concentrations on the average level of glucocorticoids during the season of growth of the hair (Millspaugh et al. 2002; Sheriff et al. 2011b).

However, many factors may affect glucocorticoid levels (e.g. review in Sapolsky et al. 2000; Millspaugh & Washburn 2004; Touma & Palme 2005; Pereira et al. 2006; Keay et al. 2006; Busch & Hayward 2009; Homyack 2010). This includes, among others, sex (e.g. in mammals and birds review in Touma & Palme 2005), age (e.g. in deer: Creel et al. 2002), season (e.g. in deer: Huber et al. 2003), diet (e.g. in black bears: von der Ohe et al. 2004) or reproductive state (e.g. in deer: Pereira et al. 2006). Interpreting changes in glucocorticoid levels may thus be challenging when intending to study a unique factor such as predation risk on animal physiology (Clinchy et al. 2011). However, this disadvantage may also become an advantage since glucocorticoid levels

reflect the level of energy required for the individual to cope with a given situation. Glucocorticoid levels integrate thus all components affecting the individual physiological balance and may be understood as a synthesis of the levels of stress perceived by the animal in a given situation within a given period of time. Therefore, glucocorticoids were sometimes referred as “energy hormone” or “stress hormone” (e.g. McEwen & Wingfield 2003; Romero & Butler 2007; Busch & Hayward 2009; Sheriff et al. 2011a)

In particular, glucocorticoids may be used to study how predation may affect deer physiology. For example, Bateson & Bradshaw (1997) studied the physiological conditions of red deer killed after a hunt with hounds. They reported that these deer had one of the highest levels of plasmatic glucocorticoid (cortisol) recorded for red deer and that it was associated to the depletion of carbohydrates of most muscles, including those not directly involved in running due to energy reallocation in presence of an emergency situation (chasing). However, in Yellowstone National Park, US, Creel et al. (2009) did not detect an effect of the presence of predation risks (ratio elk to wolves) on elk glucocorticoid levels, even though predation risk was reported to decrease elk energy intake by 27% of their maintenance requirements (Christianson & Creel 2010) and to reduce elk birth rate (ratio calves per cows) by 17% (Creel & Christianson 2008). They suggested that elk may limit physiological stress caused by predation by managing predation risks behaviorally. Indeed, elk avoided risky area limiting thus additional physiological stress (Creel et al. 2009). Similarly, Taillon & Côté (2007, 2008) reported that under low-quality diet white-tailed deer fawns on Anticosti Island, Canada, did not increase their levels of glucocorticoids but decreased their aggressiveness. Both studies highlight the close interaction between behavior and physiology. Thus, similarly to Seebacher & Franklin (2012), who suggested that physiology could be considered as a filter between the environment and the ecology of a species, behavioral adjustments may also be considered as a filter for physiological response of individuals to their environment (Wingfield 2003, 2005).

Non-consumptive effects of predation risk, inducing both behavioral and physiological adjustments, may thus be important forces shaping the relationship between prey individuals and their environment. This explains the current interest for the possibility to manage abundant large herbivore populations, like deer, in managing the levels of risk (e.g. Cromsigt et al. 2013). However, although non-consumptive effects of predation are now largely recognized for their impacts at the individual scale, their impacts at the population scale are more controversial, and more studies are needed to better assess how predation risk may affect prey population dynamic (e.g Middleton et al. 2013). In addition, food level is also a key factor limiting herbivore populations and may interact with both the consumptive and non-consumptive effects of predation (Preisser et al. 2009). Studies integrating both food and risk levels seem thus critical. This appears even more critical, considering that abundant populations of large herbivores, like deer, can affect their food resource dramatically and hence may interact with their response to predation risk.

The present study addresses this aspect and investigates how abundant deer populations manage predation risk in depleted environments, depletion they have created themselves.

III. FOUR RESEARCH QUESTIONS

To study how deer manage predation risk in heavily browsed environment, we worked on three islands of the Haida Gwaii archipelago (British Columbia, Canada). On two islands, deer have been isolated from predation and achieved high densities that resulted in a dramatic depletion of the forest understory, their main source of food (Martin et al. 2010; Chollet 2012). On the third island, deer have been hunted to reduce their density and to enable vegetation to recover at least partially (Chollet et al. in prep; Gaston et al. 2008). These islands offer thus a contrasted situation of predation risk and food: the former are safe and poor and the latter is risky and rich. We used this natural design to investigate how deer manage predation risk in contrasted situation of risk and food. In particular we considered four questions:

- 1) What resources may contribute to maintain high-density deer populations in heavily browsed environments? We addressed this question by investigating how the energy requirements of the deer population were fulfilled on each island by the resources this island could provide.
- 2) How do deer respond to low food abundance and predation risk physiologically? We addressed this question in comparing the levels of fecal glucocorticoid metabolites, an indicator of physiological stress, between the two safe/poor islands and the risky/rich island.
- 3) Have predator-naïve deer maintained anti-predator behaviors, like vigilance, in heavily browsed environments and do they still respond to predator olfactory stimuli? We addressed this question in two steps: First we studied deer vigilance levels at bait stations in contrasted situations of bait levels, habitat visibility and at day- and night-time. Then, we studied deer foraging behavior at bait station in presence of olfactory predator stimuli associated to contrasted levels of dangerousness.
- 4) How do predator-naïve deer respond to a hunting for fear experiment in a heavily browsed environment and how does it affect the vegetation? We addressed this question by investigating deer use of the hunting area via camera-traps and by monitoring the growth of four fast-growing coastal plant species. We used complementary data on deer physiological stress response, vigilance levels, flight distance, activity pattern and habitat selection to obtain a preliminary assessment of the overall effect of the hunting for fear on deer.

STUDY SYSTEM

I. HAIDA GWAI

The Islands
Lands of azure ,Northern skies
Of geese and their haunting cry,
Land of ancient monarch spruce
Of the ocean's moaning sigh.
Land of the wapitis' bugle call
Of spawning salmon streams
Land of the warrior Haida tribes
Of settler's broken dreams
Land of the trumpeter swan's retreat
Of clean, salt-laden air
Land of thunderous rolling surf,
Of otter, seal and bear
Land of the wheeling sea-gulls scream
Of shooting Northern Lights
Land of the flaming sunsets
Of soft, short summer nights
Land of the loon's mournful call
Of treasure-laden sands
Land where man can plainly see
The prints of his Maker's hands
Land that sends forth stalwart sons
Yet never sets them free
But calls them back again and again
To these Isles of the Northern Sea.

Dorothy Richardson, Tlell, Haida Gwaii, Canada, January 1966 (in Dalzell 1989)

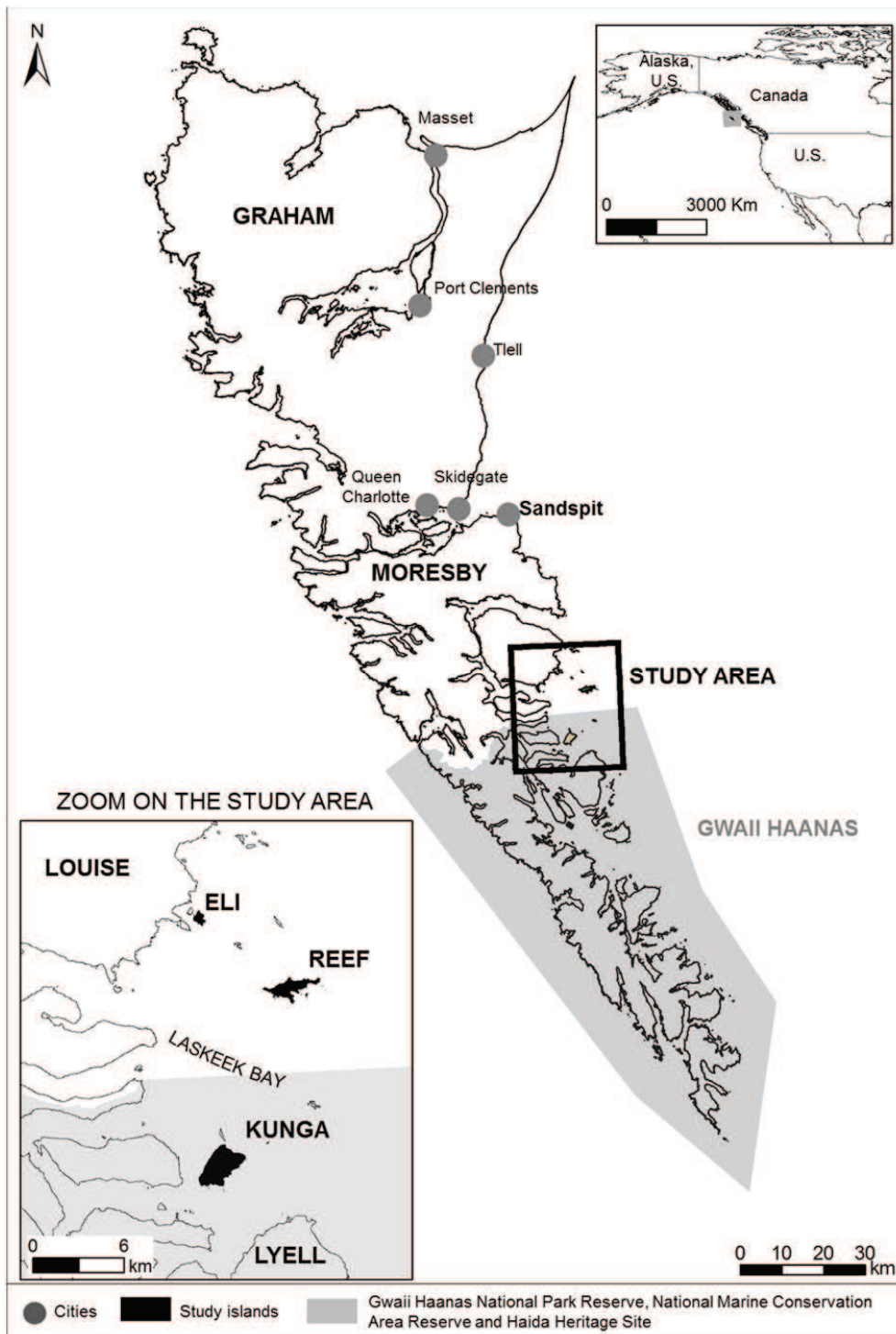


Figure 3: Study area in Haida Gwaii. Haida Gwaii is located in North Western Canada (top right panel) and four of the main islands (Graham, Moresby, Louise and Lyell islands) are identified in black capital letters. Cities are also shown. Sandspit airport weather station provided the weather data used in this study. The bottom left panel zooms on the study area (Laskeek Bay). In black are the three study islands (East Limestone (ELI), Kunga and Reef islands). Kunga belongs to Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve and Haida Heritage Site (grey area).

Haida Gwaii¹ (“Xaayda gwaay” in Haida meaning “Islands of the [Haida] People”) is an archipelago off the Northern coast of British Columbia (NW Canada: WGS84 52-54N; 131-133W). It is located over 80 km west from the British Columbian coast and 50 km South from the Alexander archipelago in South-East Alaska, US. The archipelago counts more than 350 islands. The two main islands, Graham (636 100 ha) and Moresby (339 900 ha) cover over 95% of the archipelago surface area (9 950 km²; Figure 3). Since the 1990s the southern part of the archipelago has been designated as Gwaii Haanas (“Islands of Beauty” in Haida) National Park Reserve, National Marine Conservation Area Reserve and Haida Heritage Site in order to protect, maintain and/or restore the remarkable local natural and cultural heritage (Archipelago Management Board 2012).

Between 1878 and 1925 Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) from coastal islands off the mainland were introduced on the two largest islands of the archipelago as meat supply. Most islands are now uninhabited and Haida Gwaii is devoid of the main natural predators of deer (i.e. wolf and cougar) although black bear (*Ursus americanus*), an opportunistic predator of fawns (McTaggart Cowan 1956; Ballard et al. 2001), is present on the largest islands. In this context deer colonized most islands in about 50 years (Golumbia et al. 2008) and reached the study islands over 60 years ago (Vila et al. 2004)

II. STUDY AREA

II.A. ENVIRONMENTAL CHARACTERISTICS COMMON TO THE THREE ISLANDS

II.A.1. CLIMATE AND VEGETATION

The study took place between March 2011 and October 2012 in Laskeek Bay, a group of 15 islands to the east of Moresby, and focused on three islands: East Limestone Island (41 ha: WGS84-52.91N 131.61W, thereafter East Limestone), Kunga Island (395 ha: WGS84-52.77N

¹ Previously the archipelago was officially named Queen Charlotte Islands. This name was given by Captain George Dixon, an officer of the English Navy, who explored the area in 1787. He named it after one of his ship’s name, the Queen Charlotte, which referred to the contemporary queen of Great Britain, Charlotte of Mecklenburg-Strelitz. However, this name was abandoned in the 21st century.

131.57W, thereafter Kunga) and Reef Island (249 ha: WGS84-52.87N 131.52W, thereafter Reef) (Figure 3). These three islands are located within 17 km one from another. The climate is cool temperate, oceanic, and humid-perhumid (Pojar 2008). The weather station from Sandspit airport (located 40 km north of the study area: Figure 3) recorded a mean annual precipitation of 1400 mm between 1971 and 2000. Winters are mild with average daily temperatures between 3 and 10°C between October and March and snow is rare with an annual snowfall of 62 cm and an average monthly snow depth of 1.33 cm between December and February (Figure 4). Summers are cool and moderately wet with average daily temperatures between 6 and 15°C and average monthly rainfall below 100 mm between April and September (Figure 4) (Environment Canada data).

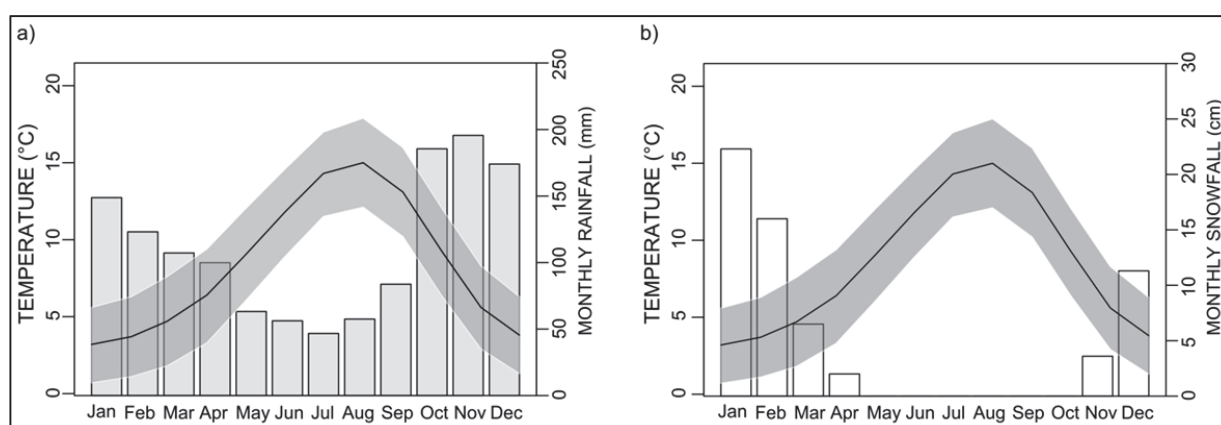


Figure 4: Average weather conditions recorded at Sandspit airport weather station between 1971 and 2000. The average daily temperature (solid line) and average minimum and maximum daily temperature (grey area around the solid line) are presented for each month. (a) Grey histogram marks the average accumulation of rainfall recorded for each month (mm). (b) Open histogram marks the average accumulation of snowfall recorded for each month (cm).

The landscape is dominated by closed coniferous forests of western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*) and Sitka spruce (*Picea sitchensis*) with some deciduous trees such as red alder (*Alnus rubra*) (Pojar et al. 1980). However, during winter 2010-2011 hurricane-force winds (>69 knots) occurred in our study area causing large windfall areas with no, or very little, canopy cover (Figure 5). In these areas, deer had access to unusual amounts of canopy foliage as supplementary food supply for a short period of time and to the regeneration of plants in this newly-created open habitat in the longer term.



Figure 5: Windfall areas on the three study islands. (a) Aerial north-western view of East Limestone (T. Husband), the yellow arrow identified a major windfall area (b) View from the northern windfall area on Kunga looking towards Laskeek Bay (north). (c) View of the north eastern windfall area on Reef. (d) Deer feeding on a fallen red cedar on East Limestone. (e) Logging work to clean the camp site on Reef (T.Verchère). (f) Logging work to ensure access and safety on critical sites in Laskeek Bay (T.Verchère).

We estimated windfall areas to cover 35, 21 and 15% of the island area on East Limestone, Kunga and Reef, respectively. These proportions were assessed via two methods: i) for each

island, we conducted boat survey to localize windfall areas. From the boat, we used handheld GPS to clarify our position and estimated the location and the extent of windfall areas on an island map with 50x50 m² squares. Then, we conducted foot survey to better define the contours of the windfall areas. Contours were recorded with handheld GPS. We combined sea- and land-surveys to map windfall areas; ii) for East Limestone and Kunga we conducted a systematic mapping of the island at a scale of 50x50 m² (Box 5). On East Limestone and Kunga the systematic survey and the contour mapping provided similar estimates of the area covered by windfall areas (4 and 9% of difference between estimates assessed with either method on East Limestone and Kunga, respectively). For consistency when comparing the three islands, we used the values assessed via the former method.

BOX 5: MAPPING OF EAST LIMESTONE AND KUNGA ISLAND

In order to study deer movements and habitat selection on the islands, we needed to better assess the distribution of deer food and shelter over the islands. Because in 2011 deer were collared on East Limestone and Kunga only, we focused on these two islands first and conducted a systematic mapping of both islands. East Limestone and Kunga mapping occurred between April and May 2012. Given our limited knowledge on how East Limestone and Kunga deer used their habitats, we decided to not use fixed habitat classes defined arbitrarily but instead used a semi-quantitative survey method similar to these used in forestry (J.L. Martin pers. comm.). We discretized the island in 50x50 m² squares, resulting in 239 and 2028 squares for East Limestone and Kunga, respectively. Because deer may commute from East Limestone to the neighboring 10-ha West Limestone, we also mapped West Limestone. This resulted in 70 additional squares surveyed in July 2012. Seven people were involved in the mapping. To limit individual biases, we calibrated our estimates by mapping some squares all together at the beginning of the mapping session. We repeated similar calibration exercise every 10-15 mapping days. In addition we also used a standard plot chart

as common reference for cover estimates (Mueller-Dombois & Ellenberg 1974).

Data collection

We located each square with handheld GPS and reached, when possible, the center of a given square to record its characteristics. For each square we first estimated the proportion of windfall and intertidal areas (i.e. beach or rocky area). Then, we considered three height strata: the canopy was everything > 25 m height, the midstory was between 1.5- and 25-m height and the understory was ≤ 1.5m (browse line in the study area: Vila & Guibal 2001).

For either the canopy or midstory strata, we estimated the cover of the tree foliage according to four cover classes: no cover, open cover for covers < 33%, medium cover for covers between 33 and 66% and closed cover for covers > 66% of the square area. We listed and ordered the three main species present in either the canopy or midstory strata according to their relative contributions to the total foliage cover in each stratum. We also recorded if red cedar and/or deciduous tree foliage were present in these strata. This informed on the possible presence of food items preferred by deer in the form of canopy subsidies (i.e. litterfall).

BOX 5 (continued)



























For the understory stratum, we estimated the cover of all vascular plants that were available to and possibly eaten by deer (i.e. all chlorophyllous plant tissues). Understory cover was recorded according to four classes: no cover for bare ground; sparse cover when food was rare and one had to search for it (e.g. annual growth from red huckleberry rhizome, sparse seedlings); low cover when food was obvious but with cover < 50% of the square; and high cover when food was abundant covering > 50% of the square area. We listed and ordered the three main species present in the understory stratum according to their relative contributions to the total understory cover.

Island maps

Many representations of the data collected are possible. Here we present two options to describe East Limestone and Kunga habitats. First, we

considered a simple habitat classification identifying only three main habitat classes, namely: forest, windfall (proportion of windfall areas $\geq 50\%$) and intertidal areas (proportion of intertidal areas > 50%). This provided a broad pattern of habitat available to deer. Secondly, we implemented these three classes by integrating information on the level of food availability, based on the presence of preferred food in the canopy subsidies and on the composition of the food available in the understory stratum. This resulted in 13 habitat classes (Table B5). Figure B5 show the associated maps. Because deer GPS data were limited in 2011 and 2012, we considered only the former map with the three main habitat classes as habitat map to study deer response to the hunting for fear experiment (see Complementary Analyses in Chapter IV).

Table B5: Habitat classes used to characterize East and West Limestone and Kunga

Symbols (map with 3 habitat classes)	Symbols (map with 13 habitat classes)	Habitat Classes
		Intertidal area
		Windfall area
		Forest with no understory and without preferred food in canopy subsidies
		Forest with no understory and with preferred food in canopy subsidies
		Forest with a sparse or low understory cover not dominated by spruce or hemlock
		Forest with an abundant understory not dominated by spruce or hemlock
		Forest with a sparse understory dominated by spruce and/or hemlock and without preferred food in canopy subsidies
		Forest with a sparse understory dominated by spruce and/or hemlock and with preferred food in canopy subsidies
		Forest with a low understory cover dominated by spruce and/or hemlock and without preferred food in canopy subsidies
		Forest with a low understory cover dominated by spruce and/or hemlock and with preferred food in canopy subsidies
		Forest with an abundant understory dominated by spruce and/or hemlock and without preferred food in canopy subsidies
		Forest with an abundant understory dominated by spruce and/or hemlock and with preferred food in canopy subsidies
		Others (e.g. canyon, cliff)

BOX 5 (continued)

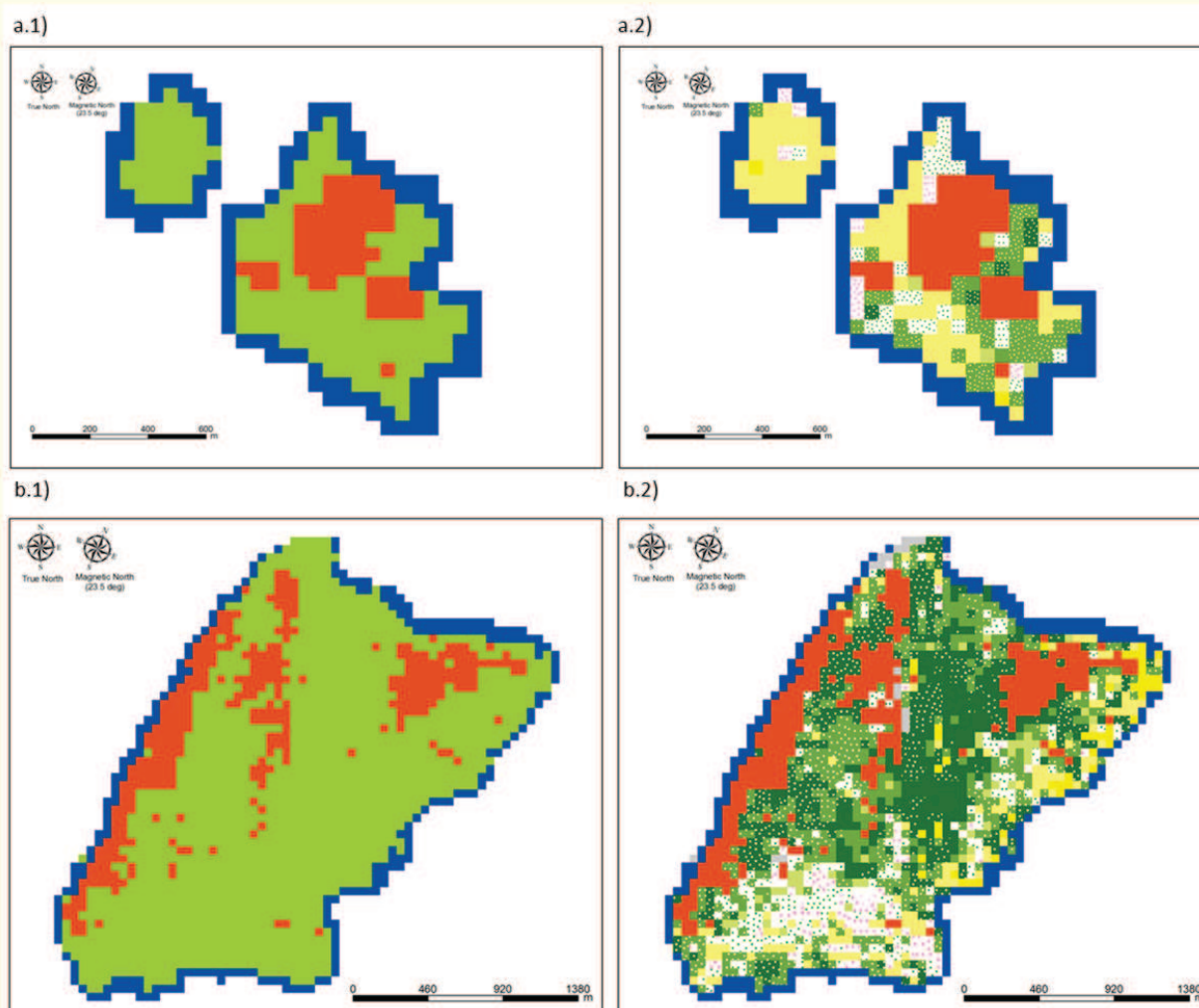


Figure B5: Habitat maps for (a) East and West Limestone and (b) Kunga. (1) The left panel presents (a.1) East and West Limestone and (b.1) Kunga maps considering only three habitat classes (intertidal area in blue, windfall areas in orange, forest in green, see Table B5); (2) The right panel present (a.2) East and West Limestone and (b.2) Kunga maps according to 13 habitat classes based on the previous three habitat classes implemented by the presence of preferred food in the canopy or midstory strata potentially available as litterfall (dotted square, see Table B5) and by the level of food and the composition of the food available in the understory stratum (legend in Table B5).

II.A.2. RISKS: BLACK BEARS AND HUMAN ACTIVITIES

Black bears are absent from the three study islands, but they are present on Louise and Lyell which face East Limestone and Kunga, respectively (Figure 3). East Limestone deer have been reported to commute between East Limestone and Louise (direct observation, GPS data) and a

bear has been reported swimming towards Kunga (Burles et al. 2004). Thus, black bears might have visited these two study islands sporadically. However, they never got established there, probably due to insufficient resources (Burles et al. 2004). In addition, black bears are generally only considered as facultative and opportunistic predators of fawns (McTaggart Cowan 1956; Hatter 1982). There is thus no strong evidence that bears represent more than a very occasional threat to adult deer and deer present during our study are very unlikely to have experienced significant predation pressure from black bears. Nevertheless, as a precaution we considered this possibility and studied if deer perceived risk in presence of black bear olfactory cues (see Chapter III). Note that bald eagles (*Haliaeetus leucocephalus*) are present but have never been reported attacking fawns on Haida Gwaii (Burles et al. 2004).

The three study islands are uninhabited and located at c. 40 km by air from the nearest town. Deer hunting is common on Haida Gwaii near populated areas. However, given the remoteness of the study islands and the abundance of deer in areas close to human settlements, sport or subsistence hunting is unlikely to occur on the study islands. Human activities are limited to research activities and to sporadic tourist visits in summer. East Limestone, however, hosts annually, from May to early July, small crews of volunteers involved in the activities of the Laskeek Bay Conservation Society, a nature conservancy society which conducts long-term monitoring of the local wildlife. Consequently, except for these and our own activities the three islands are human-free.

II.B. ENVIRONMENTAL CHARACTERISTICS SPECIFIC TO EACH ISLAND

II.B.1. THREE ISLANDS WITH CONTRASTED LEVELS OF FOOD AND RISK.

In the absence of predation (natural predators and hunting), local deer populations have reached high density estimated to be over 30 deer/km² in the study area in 1996 (Daufresne & Martin 1997). This has resulted in heavy browsing pressure reducing by more than 90% the forest understory cover when compared with islands without deer (Stockton et al. 2005). All groups of vascular plants (i.e. forbs, grasses, shrubs, trees and ferns) were impacted but not mosses which increased in cover and local diversity (Appendix I). These dramatic changes in the structure and composition of the forest understory have caused a significant decline in the

diversity and abundance of local forest bird and insect communities (Allombert et al. 2005a, 2005b; review in Martin et al. 2010).

To experimentally test the reversibility of this ecological meltdown, a cull was initiated on Reef in 1997 in order to study the response of the plant and songbird communities to a prolonged reduction in browsing pressure (Gaston et al. 2008). During the first year of the cull more than 50% of the deer population was eliminated and in 2000 (three year after the first hunt) deer density was estimated to be less than 10 deer/km² (i.e. a reduction >70% in the initial deer density : Chollet et al. in prep). Understory plants did indeed recover (Figure 6) and in 2010, when compared to 1998, plant species richness had quadrupled and the cover of the forest understory below the browse line had increased between 150 and 900% depending on the height layer considered (Chollet et al. in prep). Consequently, at the time of my study (2011 – 2012), Reef had a partially recovered understory that offered a richer and denser food supply to the remaining deer population (Chollet et al. in prep) (Figure 6)

In contrast, no cull occurred on East Limestone or on Kunga. The local deer populations have remained at high density and have maintained heavy browsing pressure on the already impoverished forest understory. Currently, the local forest understory is devoid of most plant species traditionally found in the diet of black tailed deer (Chollet et al. in prep; McTaggart Cowan 1956; Pojar et al. 1980). At the time of my study, forests on East Limestone and Kunga had a dramatically depleted, if not absent, understory mostly consisting of bare or moss-covered field layer and where the remaining plants were either below 50 cm in height (Martin et al. 2010) or with foliage above 1.5 – 2 m height, beyond the reach of deer (browse line height, Vila & Guibal 2001, Figure 6).



Figure 6: Forest understory on the study islands: (a) Recovery of the forest understory on Reef. The same plot was photographed before the first hunt (1996), 4 years later (2000) and 10 years later (2006) (J.L. Martin). (b) Example of moss-covered ground and a Sitka spruce-dominated understory on East Limestone. Spruce buds below the browse line (1.5 m) are heavily browsed by deer in spring. This results in shrub-like individuals or bonsai spruces. Spruces need c. 12, 13 years or more to escape deer browsing by reaching heights above 1.5m (Vila et al. 2002); (c) Example of bare ground on Kunga (J.L. Martin).

Thus, Reef on the one hand, and East Limestone and Kunga on the other hand, presented contrasted food levels for deer at the time of my study. For comparison, according to a 2010 plant survey, below 2-m in height the partially recovered forest understory on Reef occupied a volume at least three times higher than the one recorded on East Limestone and Kunga (Figure 7). Shrub, grass, and fern abundance was particularly contrasted, with volume indices between 12 and 166 times higher on Reef than on East Limestone and Kunga (Figure 7). Deer on Reef had

thus access to a more diverse and a more abundant food supply than deer on East Limestone and Kunga.

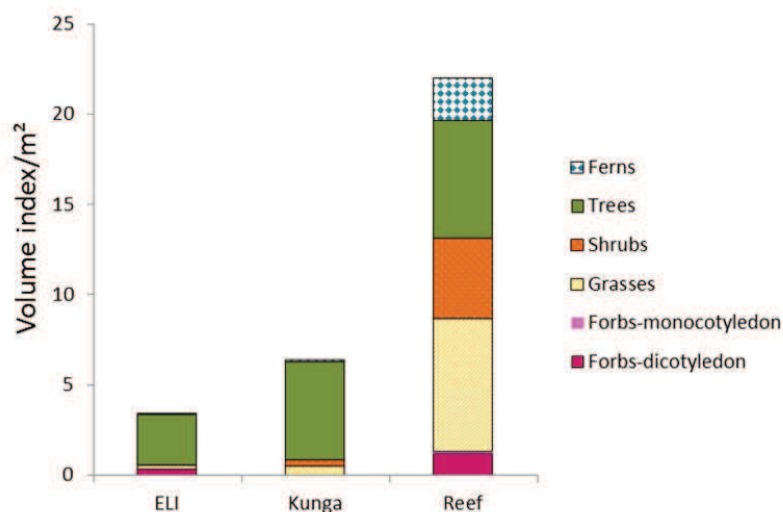


Figure 7: Composition and abundance of the forest understory on East Limestone (ELI), Kunga and Reef in 2010 (adapted from Chollet 2012). In 2010, the forest understory cover was estimated over 5 strata between 0 and 200 cm (0-5 ; 5-15; 15-50; 50-100;100-150; 150-200 cm). The volume index sum the cover estimates per square meter. For more details on the data collection,(see Stockton et al. 2005; Chollet 2012)

However, deer on Reef were also subject to higher risk levels. Indeed, since the first hunt in 1997, deer hunting has been maintained more or less regularly on Reef. Although hunting effort was reduced between 2003 and 2005, several days to weeks of hunting have occurred annually since 2006 (see Chollet et al. in prep for a summary on the hunting effort on Reef from 1997 to 2012). In particular, the last hunting events occurred in June 2010 (6 months prior to my study) and in May 2013 (7 months after the end of my study). No hunting took place during my study but researchers were present conducting various seasonal fieldwork activities (Figure 10). Because human presence was rare and possibly associated to hunting (predation risk), deer were likely to perceive humans as predators (Frid & Dill 2002). Indeed, deer on Reef usually avoided humans or flew at their sight (pers. obs.). This suggests that deer on Reef perceived humans as risk agents. Consequently, because research activities occurred on Reef during the study period, we assumed that deer on Reef perceived risk, at least when humans were present,

and hence that Reef was a risky place for deer during the study period. In contrast, deer on East Limestone and Kunga were predator-free and hence predation-risk free.

The three islands thus presented, at the beginning of the study, two contrasted situations: deer on **Reef** were exposed to predation risk (human activities assimilated to hunting) but had access to a richer and more abundant understory (**risky/rich** island), whereas deer on **East Limestone** and **Kunga** were predation-free but lived in forests with a depleted understory (**safe/poor islands**) (Figure 8).

We completed this design by conducting a hunting for fear experiment on Kunga in May 2012. This experiment aimed at studying how deer, in a depleted environment, responded to novel but limited predation risk. Within the present study, the three islands thus presented three contrasted situations of food and risk: i) on East Limestone deer had access to low levels of food in absence of risk (safe/poor island); ii) on Kunga deer had access first to low levels of food in absence of risk in 2011 (safe/poor island), then were exposed to predation risk in 2012 (moderately risky/poor island); and iii) on Reef deer had access to high levels of food in presence of risk (risky/rich island: Figure 8).

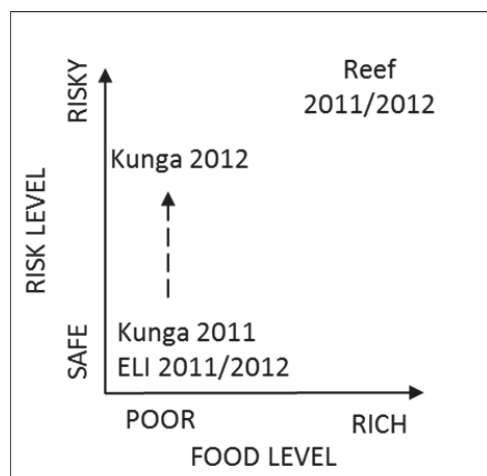


Figure 8: Contrasted levels of food (x-axis) and risk (y-axis) on the three study islands: Since the first hunt on Reef (1997), deer density has been reduced on Reef and the forest understory has recovered partially. During the study period, deer on Reef had access to a diverse and abundant forest understory as food resource (high food level – green color) but were exposed to predation risks, assimilated to human activities. On East Limestone (ELI) and Kunga deer had access to a depleted understory (low food level), but were predator-free in 2011. In 2012, we conducted a hunting for fear experiment on Kunga, exposing deer to risk, whereas East Limestone remained predation-free.

II.B.2. Deer diet in these contrasted environments.

Understory plants are usually considered as the main food resource of black-tailed deer (McTaggart Cowan 1956; Pojar et al. 1980). The fact that deer on East Limestone and Kunga have maintained dense populations for decades, despite a quasi-absent understory cover (Figure 6, 7) is intriguing.

To understand on which food deer may feed on East Limestone and Kunga, direct observations of deer were conducted on both islands in May and June 2009. Free-ranging deer were followed at a distance of c. 10-15 m. All food items consumed were recorded as well as the time spent on each items (Le Saout 2009, Appendix I). This showed that in May-June deer fed on Sitka spruce buds (in agreement with Vila & Guibal 2001) and grasses mostly. In addition, it also pinpointed that deer spent c. 10% of their foraging time feeding on tree canopy litterfall (e.g. red alder (*Alnus rubra*)) and on shoots from rhizomatous shrubs (e.g. red huckleberry (*Vaccinium parvifolium*)) or from forbs (crisp sandwort (*Stellaria crispa*)) emerging from the moss layer. Interestingly, although mosses are abundant on East Limestone and Kunga, deer do not feed on them (Appendix I). This in turn explains why in forests exposed to unrestricted browsing pressure, where all vascular plants were dramatically reduced, mosses are the unique plant group positively affected by deer and which abundance and diversity are higher on East Limestone and Kunga than on deer-free islands (Appendix I).

Because deer on East Limestone and Kunga had access to similar food resource (review in Chollet et al. submitted) and because plant species were exposed to similar browsing pressure in areas where deer were observed in 2009 (unpublished data), deer on East Limestone and Kunga were expected to have similar diet. This was confirmed by micro-histological and isotopic analyses which were conducted in 2013 on fecal samples collected in June and October 2011 and March 2012 (Poilvé 2013). In addition, in accordance with field observations of deer feeding on seaweed (Le Saout 2009), Poilvé (2013) showed that deer consumed seaweeds especially during fall and winter with quantities ranging from 0 to 13% of deer fecal material. Poilvé (2013) also highlighted that deer diet on Kunga was richer in western hemlock and seaweeds whereas deer diet on East Limestone was richer in redcedar, probably harvested in windfall areas from the 2011 storm.

In contrast, as expected for deer living in forests with richer and denser understory, deer diet on Reef was richer in dicotyledons (shrubs, forbs) than in conifers (Poilvé 2013). This was in agreement with a previous study on browsing frequencies of understory plants conducted on Reef in 2009 (Le Saout 2009). In this study, shrub, fern and grass species were the main browsed species, whereas coniferous trees (except for redcedar) were less affected by deer. Micro-histological analyses also showed that deer on Reef consumed less seaweeds in winter (c. 0-4% of deer fecal material), which is likely to result from the higher availability of terrestrial food offered by the partially recovered forest understory (Poilvé 2013).

III. DEER CAPTURE

We captured deer under BC Wildlife Act Permit NA11-68421. On East Limestone and Kunga, capture sessions occurred in March-April 2011 and August-October 2011 and 2012. On Reef, capture sessions occurred in March-April 2012 and August-October 2011 and 2012. We captured deer with baited boxtraps, except for two captures in March-April 2011 when individuals were netgunned from the ground.

Boxtraps were 1.5-m deep, 1-m wide, 1.2-m high made in 1-cm fir plywood (Figure 9a-c). Bait consisted in 4-5 apples and c. 500 g of cob (ProForm Cob, Viterra Feed Products, Chilliwac, BC, Canada). We equipped most boxtraps with VHF transmitters. We monitored each boxtrap occupancy directly or remotely via the beat of the VHF signal (Figure 9b). This was done at least every 6 hours at daytime, and at dusk and dawn. Once captured, we ear-tagged deer for identification, recorded information about deer health, reproductive state, physiology, morphometry and body mass (Figure 9e, but see Chapter III, Methods for complementary details on boxtrap management and deer handling). We equipped deer heavier than 20 kg with a GPS collar (Lotek S 7000) so that the GPS collar mass (c. 420 g) would represent less than 2% of the deer body mass.



Figure 9: Deer capture method using boxtrap. (a) Construction of a boxtrap on East Limestone (T. Verchère). (b) The boxtrap door is fixed. The yellow arrow points the VHF transmitter enabling to monitor the boxtrap remotely. (c) Example of an active boxtrap: i.e the trap is baited and triggered, ready to catch a deer. Some bait is also placed in front of the trap to attract deer. (d) A captured deer leaves the boxtrap and is caught in a net (nylon net, 38-mm mesh size, 2-mm string diameter, J.L. Martin). (e) The individual is weighted in the net with a blind fold on the head (T. Verchère). (f) The individual is maintained on the ground and is equipped with ear-tag and possibly with a GPS collar (J.L. Martin). In addition, during deer handling, we also measured deer hind foot length and collected a piece of ear tissue (c. 4 mm²) for future DNA analyses, hair sample from the shoulder and/or the tail and feces samples. In the present study, only deer body mass and GPS data are directly considered in the analyses.

Overall we captured 24 deer on East Limestone (10 females and 14 males), 22 on Kunga (11 females and 11 males) and seven on Reef (3 females and 4 males: Box 6). These captures provided a first insight on the local demography of deer on each island (Chapter I). However, note, that most data analyzed during my study were acquired between April 2011 and July 2012 and hence included only 17, 18 and four marked deer on East Limestone, Kunga and Reef, respectively (Box 6). Among these deer, eight and seven adult females were equipped with GPS collars on East Limestone and Kunga, respectively, whereas only two males were equipped with GPS collars on Reef (Figure 9). Because males and females may differ in their spatial behavior (e.g. Clutton-Brock et al. 1987; Beier & McCullough 1990; Weckerly 1993; Mysterud & Østbye 1999; Alldredge & Griswold 2006) we considered only GPS data for collared females on East Limestone and Kunga (Figure 9).

BOX 6: DEER RESPONSE TO CAPTURE ACTIVITY

To capture deer we used c. 10-15 different boxtrap locations on each island. Capture success varied among islands. For example in August-October 2011, capture success, estimated as the number of captures per active boxtrap per day, was ten times higher on East Limestone and Kunga than on Reef (mean \pm sd: East Limestone: 0.4 ± 0.5 capture/boxtrap/day; Kunga: 0.2 ± 0.3 capture/box/day; Reef: 0.03 ± 0.07 captures/box/day) (Figure B6.1).

Remarkably, during a single capture session, deer could be recaptured several times. For

example in August-October 2011, more than 50% of deer were captured at least three times on East Limestone and Kunga, with an average number of captures for these deer of 12 ± 7 and 10 ± 7 on East Limestone and Kunga, respectively. During the same capture session only two individuals were captured on Reef (Figure B6.2), among which one was recaptured 14 times (Figure B6.1) whereas the other one was never recaptured. This suggests that deer may adopt different strategies in presence of baited boxtrap.

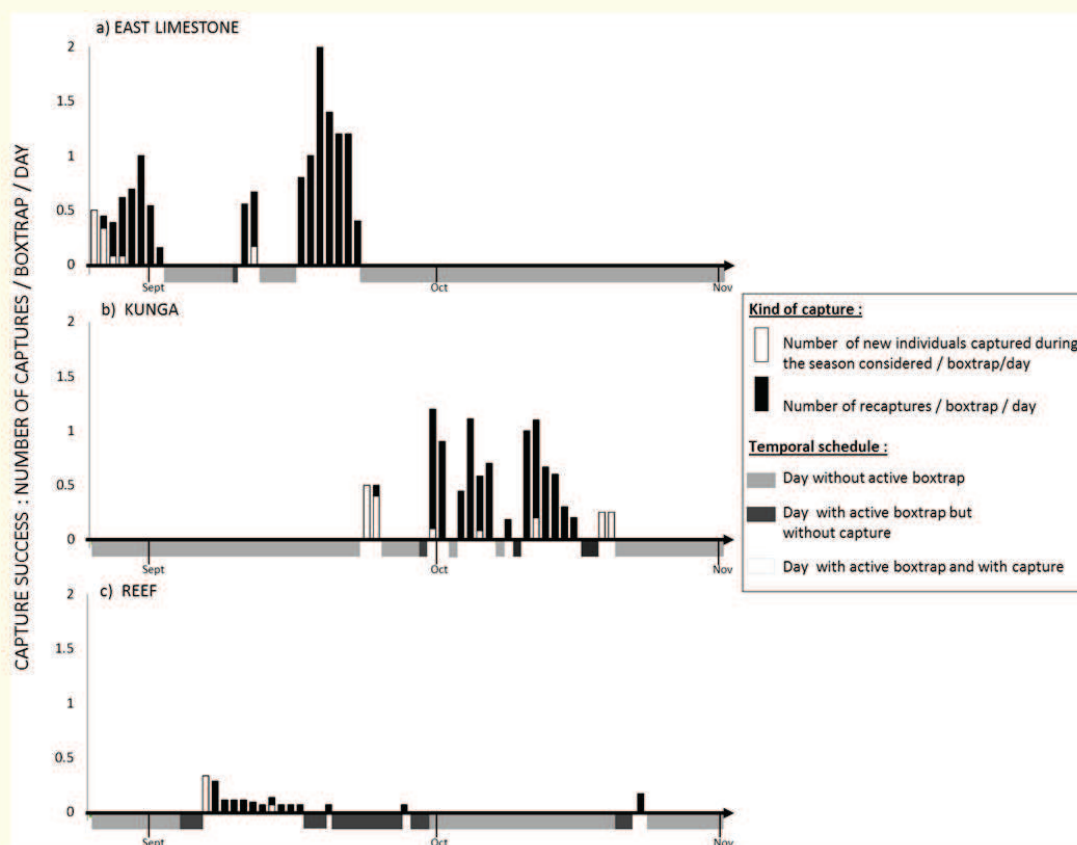


Figure B6.1: Capture success on (a) East Limestone, (b) Kunga and (c) Reef in August-October 2011. The number of first captures (open bars) or recaptures of individuals caught earlier (closed bars) during the capture session considered are shown in relation to date. Each bar corresponds to a given day. Capture days are identified by three shades: grey shades below the x-axis mark days when no boxtraps were active; black shade mark days when at least one boxtrap was active but no capture occurred and the absence of shade marks days when boxtraps were active and captures occurred.

BOX 6 (continued)

Interestingly, a similar pattern was found between capture sessions (Figure B6.2). On East Limestone and Kunga, more than 50% of deer captured in either March-April or August-October 2011 were recaptured in August-October 2011 or in August-October 2011 or in August-October 2012 (Figure B6.2). Among them, c. 30 and 80% were adult females in 2011 and 2012, respectively. This increase in the number of recaptured adult females was likely due to a higher proportion of already marked adult females in the area. On East Limestone, 43% of newly captured deer were fawns during both sessions of August-

October in 2011 and in 2012 and other newly captured deer were either adult females (57% in 2011) or males (43% in 2012). On Kunga, fawns accounted only for less than 20% of newly captured deer during both fall sessions. Adult females (37% in 2011) and/or adult males (37% in 2011 and 60% in 2012) accounted for the other newly captured deer. Different proportion of sex and age classes recaptured between the sessions of March-April and the ones of August-October might be related to seasonal changes in deer behavior and/or interest in bait.

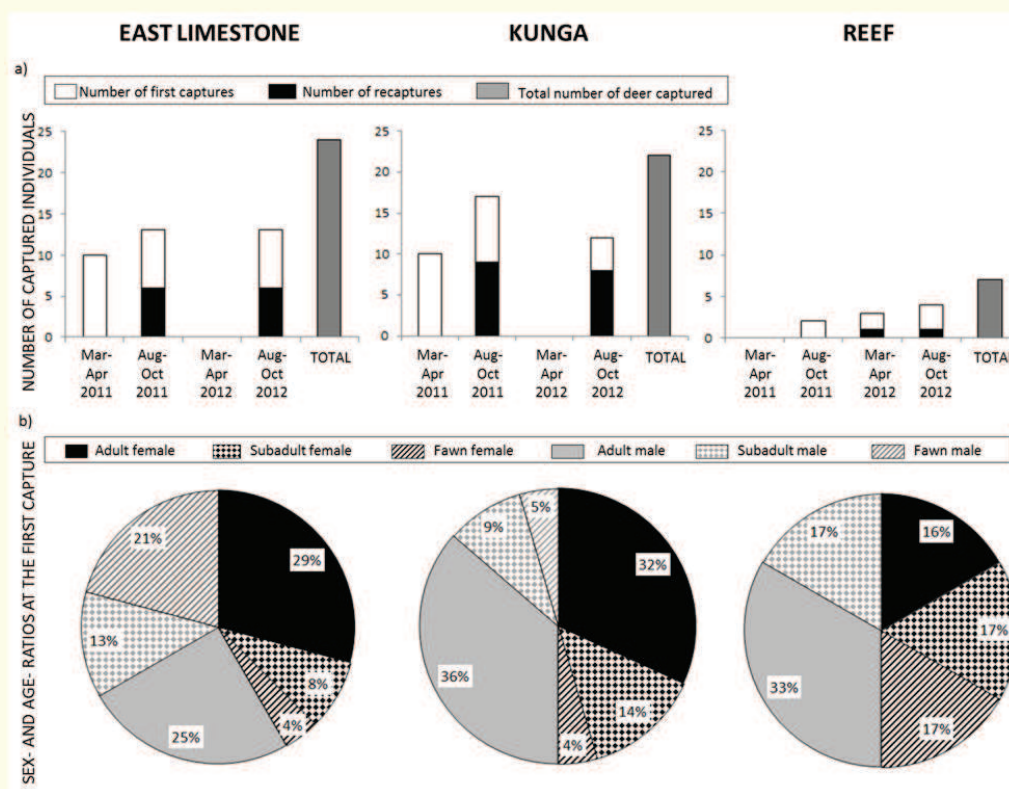


Figure B6.2: Number and sex- and age-classes of deer captured during the capture sessions on East Limestone, Kunga and Reef. (a) For each island (column), the number of individuals captured during each capture session is provided. Open bars report the number of deer capture for the very-first time (never captured before). Closed bars report the number of deer already captured during previous sessions and recaptured during a given session. The grey bars indicate the total number of deer captured on each island over all capture session (i.e. sum of the white bars). (b) The proportions of adults (> 27 month-old deer: filled form), subadults (10 – 27 month-old deer: dots) and fawns (<10 month-old deer: hatched form), females (black) and males (grey) are provided. These proportions were calculated from the total number of individuals captured on a given island and from the individual age-class at its very-first capture (when a given individual was ear-tagged).

BOX 6 (continued)

More than half of the deer could thus be recaptured within and across capture sessions, including remarkably high frequency of recaptures (> 5 recaptures/deer/capture session for > 40% of deer on East Limestone and Kunga, with a respective maximum of 13 and 19 recaptures/capture session for a given individual). This suggests that most captured deer seem to handle the capture experience nicely, or at least that they trade-off the capture for the opportunity to gain a meal and human disturbances. Nonetheless, some unmarked deer could still be observed on the island after all captures, indicating that they were never caught in boxtraps.

This may be explained by two non-exclusive hypotheses: on the one hand, boxtraps are novel objects for deer and unmarked deer may be shyer and avoid boxtrap due to neophobia (Réale et al. 2007). On the other hand, boxtraps are also associated with odors from humans and deer previously captured. Unmarked deer may have assessed or responded differently than marked deer to the trade-off between the opportunity to gain a meal and risks associated to humans (Lima & Dill 1990). Both hypotheses

highlight inter-individual differences in temperament, physiological state and/or risk- and gain- perception between unmarked and marked deer. Because variability in recapture rates also exists among marked deer, deer response to capture may be understood as a behavioral gradient between easily-recaptured deer, highly tolerant to human disturbances, and never-captured deer (unmarked deer), less tolerant to human disturbances, with a continuum of marked deer more or less tolerant in between. Such a gradient (from shy to very shy) is also likely to exist within unmarked deer, although it is not accessible with capture data. Because marked deer were captured at least once, relatively less-tolerant marked deer are still expected to be more tolerant to human disturbance than unmarked deer (never captured). Therefore, for simplification, we identified two kinds of deer as function of their response to human disturbances: i.e. the more-tolerant marked deer vs. the less-tolerant unmarked deer. Both kinds of deer are considered separately in the study of the effect of the hunting for fear experiment on deer behavior.

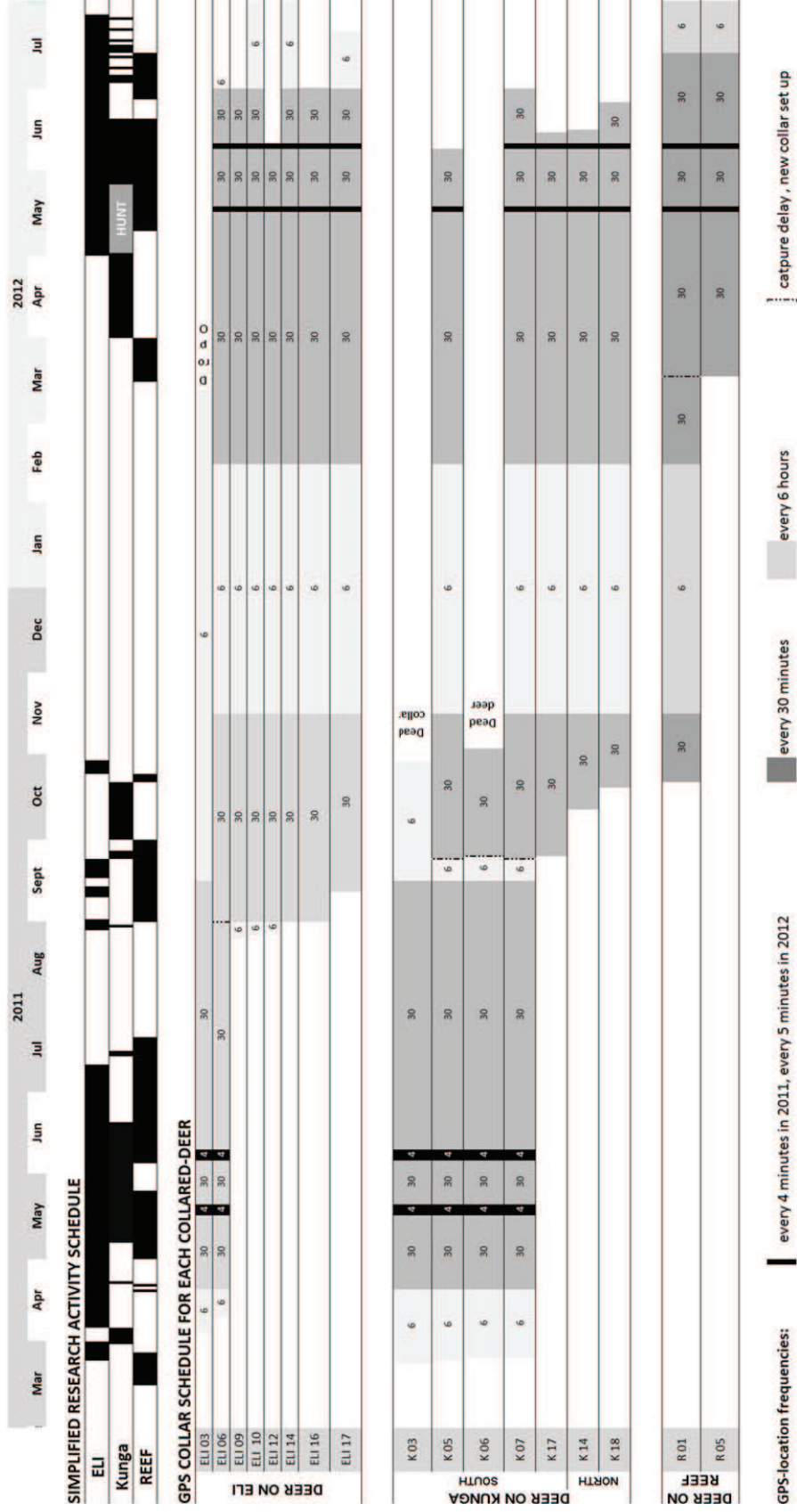


Figure 10: Simplified research activity schedule and GPS schedule for collared deer on the three islands (East Limestone, Kunga and Reef) between March 2011 and July 2012 (main study period). Periods with research activities on a given island are marked in black. The period of the hunting for Kunga and Reef, respectively (May 1 to May 26, 2012) is highlighted in red. During the main study period eight, seven and two deer were collared on East Limestone, Kunga and Reef, respectively. GPS location frequencies are given for each GPS-collar with a gradient from dark colors for high-frequencies (every 4—5 minutes) to light colors for low frequencies (every 6 hours). When we equipped a deer with a new collar it is marked by a fine vertical black bar. On the whole, nine, ten and three GPS collars were set on East Limestone, Kunga and Reef, respectively. During the study period, only males were captured (and collared) on Reef whereas only females were collared on East Limestone and Kunga. On Kunga two collared females we caught in the north of the island and the five others were caught in the south of the island.

**CHAPTER I:
UNDERSTANDING THE PARADOX OF DEER PERSISTING AT
HIGH ABUNDANCE IN HEAVILY BROWSED HABITATS**

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“To estimate (ii) the biomass provided by the ‘understory fluxes’, we used 2.25-m² x 1.8-m high exclosures. [...] To estimate (iii) the biomass provided by the ‘canopy subsidies’, we used 1-m² litterfall traps set at 2 m above the ground in forest areas” – Chapter I, Material & Methods



Figure A: Fieldwork settings to measure the biomass of the annual growth of understory plants and to estimate the litterfall biomass. (a) Exclosure (black fence) and litterfall traps (green net) were prepared at camp site and carried over the islands to their final location. (b) Example of an exclosure (yellow arrow in the foreground) and of a litterfall trap (yellow arrow in the back ground) set on Reef. (c) Removal of understory biomass in a windfall area on East Limestone in May 2011 (T.Verchere).

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CHAPTER I: UNDERSTANDING THE PARADOX OF DEER PERSISTING AT HIGH ABUNDANCE IN HEAVILY BROWSED HABITATS

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KEYWORDS: black-tailed deer, energy balance, overabundant deer, negative feedback

ABSTRACT

In the context of remarkable increases in many deer populations observed in temperate forests, it is critical to better understand the processes sustaining abundant populations despite dramatic declines in the vegetation they feed on. When natural predation and hunting levels are too low to control deer populations, a resource-driven negative feedback is expected. Such a feedback assumes that the remaining resources do not match the energy requirements of a current herbivore population, thereby limiting herbivore abundance. Here we take advantage of a well-documented, long-term study of abundant predator-free populations of black-tailed deer *Odocoileus hemionus sitkensis* on the Haida Gwaii archipelago (Canada) to assess the ability of a heavily browsed forest habitat to sustain abundant deer populations. For two deer populations, we: (i) compared the energy provided by various resource pools to the energy required by deer; and (ii) identified what components of the environment contributed most to support them. Qualitatively, our results are robust to the many assumptions and uncertainties and identify the resources currently available that allow these abundant deer populations to meet their energy needs despite the apparent paucity in resources. Resources are provided by a flux of hardly visible plant tissue produced by perennial species highly tolerant of herbivory and able to survive via underground structures (e.g. rhizomes), and by subsidies provided by canopy trees or by plants in refuges (i.e. litterfall and seed bank). We discuss the possibility of a resource-driven feedback that may ultimately occur in the long term as a result of changes in recruitment, productivity and fertility of plants. The possible lack of resource-driven feedback in the short or medium term should be considered by managers when assessing the need for active deer population control in situations without carnivores or hunting.

INTRODUCTION

The current growth of large herbivore populations in temperate forests has significant ecological and socio-economic impacts (e.g. changes in forest regeneration, crop damage, Rooney & Waller 2003, Côté et al. 2004). A better understanding of the factors limiting these populations can contribute to improving management strategies. Limits to population growth depend on a combination of both “top-down” (descending control of predators on their prey) and “bottom-up” (ascending control of available resources on their consumers) processes (e.g. Bonenfant et al. 2009, Ripple & Beschta 2012, Forrester & Wittmer 2013).

In many places of the northern hemisphere, natural predators have been reduced and/or habitats have been altered in favor of herbivore populations. Current levels of natural predation and hunting are often too low to exert significant control on large herbivore abundance (Crête & Daigle 1999). In this situation, deer populations are most likely limited by direct effects of harsh climatic conditions and/or a lack of resources via a resource-driven, density-dependent, negative feedback (Sæther 1997, Simard et al. 2008, Bonenfant et al. 2009). The speed at which such a feedback occurs depends on how quickly the total population impact translates into lower resource production. This in itself is linked to the time needed for the herbivore impact to affect the plant demographic stage that provides resources to the herbivore. Defoliation has an immediate impact on resource availability, but further resource decline may occur with habitat changes linked to slow-paced effects on plant demography (Bardgett & Wardle 2003). However, the magnitude and dynamics of these effects is not necessarily easy to quantify. Whereas palatable small-sized shrubs and forbs may be quickly overbrowsed leading to a short-term decline in this resource (e.g. Horsley et al. 2003), some herbaceous vegetation can also be strongly defoliated but their relatively inaccessible meristems ensure rapid regrowth and thus little impact on short-term plant demography (e.g. Rooney 2009). Other resources, such as tall-tree canopy litterfall subsidies, reported for black tailed deer on Vancouver Island, Canada (Rochelle 1980), for white-tailed deer *Odocoileus virginianus* on Anticosti Island, Canada (Tremblay et al. 2005) and for sika deer *Cervus nippon* in Japan (Takahashi & Kaji 2001), may also contribute to sustaining ungulate populations in heavily browsed environments with little effect on short- or medium-term reduction in resource production. The link between a strong

reduction in apparent resource abundance and herbivore abundance may therefore deserve closer attention.

Here we investigated the resources that sustain unchecked deer populations where most adult females reproduce despite a severe reduction in understory vegetation available to them. We took advantage of the exceptional situation offered by some islands of the Haida Gwaii Archipelago (British Columbia, Canada), where introduced Sitka black-tailed deer *Odocoileus hemionus sitkensis* have maintained high-density populations for decades despite dramatically browsed forest understories (Stockton et al. 2005, Martin et al. 2010). Introduced over 100 years ago to the northern part of the archipelago, deer colonized most of the islands in less than 50 years. They severely reduced tree regeneration (Stroh et al. 2008) and eliminated over 90% of the understory plant cover (Stockton et al. 2005), affecting animal communities that depend on understory vegetation (insects and birds: Martin et al. 2010). Although a population crash was documented on Haida Gwaii in the 1940s following the initial population explosion, deer densities have remained high since the 1950s (Golumbia et al. 2008) and were estimated to be more than 15 deer / km² (Martin & Baltzinger 2002). With such dense populations and their impacts on native ecosystems, deer are a major concern for land management on Haida Gwaii (Golumbia et al. 2008).

To assess how this heavily browsed landscape is able to sustain the local deer populations, we measured the biomass of available plant resources, converted it to available energy, and then compared available energy to a model-based estimation of energy requirements of the deer populations based on previous detailed energy studies conducted on *Odocoileus* sp. in similar habitats (e.g. in Alaska, Hanley 1984, Parker et al. 1999, Hanley et al. 2012).

I. MATERIAL & METHODS

I.A. STUDY AREA

The study took place on two islands of Laskeek Bay on the eastern coast of the Haida Gwaii Archipelago (British Columbia, Canada): East Limestone (41 ha: WGS84-52.91N 131.61W) and Kunga (395 ha: WGS84-52.77N 131.57W). The climate is cool temperate, oceanic, and humid-perhumid (Pojar 2008). The weather station in Sandspit (located 40 km north of the study sites) recorded a mean annual precipitation of 1400 mm with average monthly rainfall below 200 mm between 1971 and 2000. Summers are cool and moderately wet with average daily temperature between 6 and 15°C and monthly rainfall < 100 mm. Winters are mild with average daily temperatures between 3 and 10°C between October and March and snow is rare with an annual snowfall of 62 cm and an average monthly snow depth of 1.33 cm between December and February (Environment Canada data).

The landscape is dominated by closed coniferous forests of western hemlock *Tsuga heterophylla*, western redcedar *Thuja plicata*, and Sitka spruce *Picea sitchensis* with some deciduous trees such as red alder *Alnus rubra* (Pojar et al. 1980). These study islands were colonized and heavily browsed by deer for more than 60 years (Vila et al. 2004). All groups of vascular plants (i.e. forbs, grasses, shrubs, trees and ferns) have been dramatically impacted by deer (Stockton et al. 2005) but not mosses, which are not consumed by deer and which have actually increased in cover (Chollet et al. submitted). This herbivory has resulted in closed-canopy forests with a depleted understory, where the remaining plants are mostly <50 cm in height (Martin et al. 2010), and with bare or moss-covered ground lacking in most plant species usually recognized as essential in the diet of black-tailed deer (McTaggart Cowan 1956, Pojar et al. 1980).

In the winter 2010-2011 hurricane-force winds (>69 knots) occurred in our study area causing large windfall areas with no, or very little, canopy cover over 35 and 21% of the area on East Limestone and Kunga islands, respectively. As a consequence, this study considered available plant resources to deer under two habitat scenarios: in the absence and in the presence of windfall areas.

I.B. ENERGY BALANCE

We compared the yearly amount of energy available to and required by the local deer populations by considering two seasons: summer (from April to September) and winter (from October to March) in consistency with the seasonal changes in deer pelage (McTaggart Cowan & Raddi 1972). For each season we estimated the resources available and required using two models: the resource and the deer models.

I.B.1. RESOURCE MODEL

I.B.1.a. Resource description

We identified three pools of resources that could contribute to sustaining deer populations: (i) “understory”; (ii) “understory fluxes”; and (iii) “subsidies from the canopy”.

(i) We defined the “understory” resource as the biomass of vascular plants that were available to and possibly eaten by deer. These included all chlorophyllous plant tissues (green plant parts) <1.5 m in height (the browse line height in our study area: Vila & Guibal 2001). For Sitka spruce, deer feed almost exclusively on buds and fresh shoots available in spring (Vila & Guibal 2001), therefore we only included these plant-parts in our estimates.

(ii) We defined “understory fluxes” as the biomass of vascular plants growing in the field layer each year. These fluxes included the yearly growth of green plant parts from both perennial rhizomatous plants species “hidden” in the moss layer (e.g. red huckleberry *Vaccinium parvifolium* or crisp starwort *Stellaria crispa*) (Chollet 2012) and from young individuals emerging from the seed bank (e.g. red alder or Sitka spruce seedlings).

(iii) We defined the “canopy subsidies” as the biomass that falls from the canopy and becomes available to deer. These subsidies included leaves from deciduous trees, redcedar sprays, buds from adult spruce and lichens (Parker et al. 1999, Tremblay et al. 2005, Le Saout 2009).

Given the similarity in environmental conditions between East Limestone and Kunga islands (Pojar et al. 1980, Martin et al. 2010) and given similar prevalence of recent windfalls on both

islands, we assumed that levels of “understory fluxes” and “canopy subsidies” were comparable on both islands. For each of these resources, we estimated average available biomass per unit area by pooling the data from both islands.

I.B.1.b. Biomass Assessment

To estimate (i) the annual biomass provided by the “understory” resource, we collected the available biomass (as defined above) in five 1-m² plots, located along 40-m transects between June and July 2011. On each island, we monitored 10 transects in the intact forest areas and 12 transects in the windfall areas. To estimate (ii) the biomass provided by the “understory fluxes”, we used 2.25-m² x 1.8-m high exclosures. In intact forest areas we monitored four and six such exclosures on East Limestone and Kunga islands. In windfall areas, due to logistic constraints, we monitored four exclosures on East Limestone only. Of those, one was destroyed during the winter 2011-2012. In May 2011 we removed all green biomass from a 1-m² field-layer in each exclosure and a year later, in May 2012, we collected the biomass that had grown over the year in these exclosures. To estimate (iii) the biomass provided by the “canopy subsidies”, we used 1-m² litterfall traps set at 2 m above the ground in forest areas, with four traps on East Limestone and six on Kunga. We collected the monthly biomass fallen in each trap in June and July 2011.

We dried and weighed the biomass collected by species in each sampling unit. Masses <0.1g were counted as zero. For each type of resource and habitat (intact forest and windfall), we estimated the average annual dry matter per m² for each species. For the canopy subsidies we assumed that the monthly dry matter per m² was constant over the period of availability of each species (cf. section below) in order to calculate the annual dry matter per m².

We assumed that the biomass produced in exclosures was comparable to the situation experienced by plants exposed to regular browsing. Indeed, whereas the exclosures may overestimate the biomass produced by plant growth growing once a year (e.g. Sitka spruce buds), they may underestimate the biomass produced by plants that respond positively to browsing (e.g. grasses: Augustine & McNaughton 1998). In our study more than 97% of the dry biomass collected came from plant species tolerant to browsing through the presence of

rhizomes, basal meristems and/or high shoot densities (Table I.3) that facilitate regrowth after browsing events (Pojar & MacKinnon 1994). In addition, our field observations confirmed that most browsed plants regrew during the same season. Therefore, we assumed that the biomass produced in exclosures, if not underestimated, should be at least comparable to the biomass produced by plants exposed to regular browsing.

I.B.1.c. Estimation of available energy

For each habitat scenario (i.e. in the absence or presence of windfall), we estimated for each season (i.e. winter and summer) the energy available to the deer populations in two steps. First, we estimated the amount of energy provided by each resource at a 1-m² scale. Secondly, we assessed the energy provided by each resource and by the sum of all resources at the scale of individual islands. In the absence of windfall, forest habitat was considered to include the entire island area. When windfall areas were incorporated in the scenario, forest habitat covered 65 and 79% of East Limestone and Kunga islands, respectively, and windfall habitat covered the remaining extents.

We estimated the seasonal energy provided by each resource at a 1-m² scale as follows. First for each species per resource, we multiplied its annual dry matter per m² by the proportion of days that it was available during each season (Equation 1). We then multiplied this value by the seasonal metabolizable energy content of the given species. We assessed the seasonal amount of energy per m² provided by each resource by summing the amounts of energy provided by all species present in a given resource (see Equation 1). The proportion of days when a species was available for deer was added to the model because some plant species were not available as a food resource throughout the year (e.g. deciduous trees, forbs: Pojar & MacKinnon 1994). In particular, we considered that annual understory fluxes were restricted to the summer season because most plant growth occurs in summer (Pojar & MacKinnon 1994).

For each habitat scenario (with or without windfall), we estimated the seasonal amount of energy provided by each resource at the island scale as follows: First, we multiplied the seasonal amount of energy per m² of each resource by the habitat area (forest or windfall) where the

resource occurred. Then, we summed these values over all resources present on the island to estimate the seasonal energy value (SEV) of the island for deer (Equation 1).

$$SEV = \left(\begin{array}{l} \left(\sum_{\text{plant sp } i}^{\text{nr}} \alpha_{i,\text{season}} \bullet DM_{ri} \bullet ME_{i,\text{season}} \right)_{r=\text{understory}} \bullet A_{\text{forest}} \\ + \left(\sum_{\text{plant sp } i}^{\text{nr}} \alpha_{i,\text{season}} \bullet DM_{ri} \bullet ME_{i,\text{season}} \right)_{r=\text{understory.fluxes}} \bullet A_{\text{forest}} \\ + \left(\sum_{\text{plant sp } i}^{\text{nr}} \alpha_{i,\text{season}} \bullet DM_{ri} \bullet ME_{i,\text{season}} \right)_{r=\text{canopy.subsidies}} \bullet A_{\text{forest}} \\ + \left(\sum_{\text{plant sp } i}^{\text{nr}} \alpha_{i,\text{season}} \bullet DM_{ri} \bullet ME_{i,\text{season}} \right)_{r=\text{windfall.understory}} \bullet A_{\text{windfall}} \\ + \left(\sum_{\text{plant sp } i}^{\text{nr}} \alpha_{i,\text{season}} \bullet DM_{ri} \bullet ME_{i,\text{season}} \right)_{r=\text{windfall.understory.fluxes}} \bullet A_{\text{windfall}} \end{array} \right)$$

(Equation 1)

where DM_{ri} is the annual Dry Matter per m^2 of the plant species i in the resource r ($\text{kg} \bullet \text{DM} \bullet \text{m}^{-2} \bullet \text{year}^{-1}$), $ME_{i,\text{season}}$ is the Metabolizable Energy content of the species i in a given season ($\text{kJ} \bullet \text{kg}^{-1} \bullet \text{DM}$), $\alpha_{i,\text{season}}$ is the proportion of days of availability of the species i during a given season (i.e. the number of days when the species i is available during the season divided by the total number of days when the species i is available over the year), and A_{forest} and A_{windfall} are the habitat areas where the resource occurred under the habitat scenario considered (m^2). Under the scenario not accounting for windfalls A_{forest} is the island area and A_{windfall} is zero; under the scenario accounting for windfalls A_{forest} and A_{windfall} are the respective forest and windfall areas estimated for each island.

Energy contents (Appendix I.A) were obtained from Seip (1979), Parker et al. (1999), Munger (2002) and Haley et al. (2012), and seasonal estimates were assessed as follows : (i) when available, we used the seasonal digestible energy content of each plant species; (ii) when seasonal data were lacking, we used the same value for both seasons; and (iii) when data on a given species were lacking, we used the average seasonal content of other species from the same genus, family or guild in this order of preference, and according to their availability in the literature. We then estimated the amount of metabolizable energy as the digestible energy contents corrected by a factor of 0.80 (average value of the metabolizable energy coefficients

estimated for *Odocoileus* sp for hay, deciduous and conifer browse: Robbins 1993). Appendix I summarizes for each species the seasonal availability and energy contents used in this model.

I.B.2. DEER MODEL

I.B.2.a. Deer demographic parameters

To estimate the energy requirements of East Limestone and Kunga deer populations, we considered both sexes and three age classes: adult (>27 months old), subadult (10- 27 months old) and fawn (<10 months old). Fawns became thus subadults after their first winter and subadults became adults before their third winter. We identified five parameters to describe the local deer populations: (i) population abundance; (ii) sex ratio; (iii) age ratio; (iv) body mass of each sex and age class; and (v) reproductive investment of each sex and age class.

(i) We estimated the abundance of East Limestone and Kunga deer populations by a capture-mark-recapture (CMR) method using camera-trap data. In July and August 2012, we used motion sensor cameras (RECONYX PC 900) to survey six sites over 40 days on East Limestone and 29 sites over four sessions of four to six days on Kunga. For each picture we aged, sexed and identified individual deer whenever possible. We recorded 218 and 103 deer visits on East Limestone and Kunga, respectively. We used a recently developed spatially-explicit CMR approach (Chandler & Royle 2013) to estimate the local deer abundance. This new method has the appealing advantage that it accommodates both identified and unidentified individuals. A detailed description of the models used is available as supplementary information (SM.I.1). We estimated that a month after the beginning of the birth season deer abundance was approximately 36 deer (95% CI: 30; 44) on East Limestone (i.e. 88 deer/km², [95% CI: 73; 107]) and 168 deer (95% CI: 42; 536) on Kunga (i.e. 43 deer/km², [95% CI: 11; 136]). The large confidence interval around the Kunga estimate resulted from a shorter survey and a lower proportion of marked deer (SM.I.1). Nevertheless, the confidence interval for Kunga includes possible densities for East Limestone. This is in agreement with previous research showing that both islands are exposed to comparable deer browsing pressure (Chollet 2012).

(ii & iii) We estimated sex and age ratios from the camera-trap survey. We considered only pictures with either sexed or aged individuals to estimate the proportion of each sex or age class in the populations. We assumed that sex ratios were constant across age classes and seasons. We considered that adult numbers were constant over the year and that fawns became subadults at the end of the winter (Table I.2).

(iv) We estimated the average body mass of each sex and age class for each season from deer captures during which we sexed, aged, weighed and ear-tagged individuals. Captures took place in March-April 2011 and August-October 2011 and 2012. We captured 24 individuals on East Limestone (10 females, 14 males) and 22 individuals on Kunga (11 females, 11 males). We used the data from August-October and March-April captures as equivalent to summer and winter body mass, respectively. Data from March-April captures were too limited to assess winter body mass of female and male subadults (16 to 21 month-old individuals in winter). We used the average body mass of 15-, 16-month old individuals captured in August-October instead. We considered that body mass was constant over a season.

(v) We estimated the investment of females in reproduction during August-October captures via their reproductive status (i.e. lactating or non-lactating). On both islands 80% of the captured adult females were lactating and only one subadult female of the three captured was lactating. Moreover, during the camera-trap survey, adult does had either no fawn or only one fawn. A single case of possible twins has been observed on East Limestone over the last 5 years (SLS. pers. obs.). Thus, to simplify, we considered that only adult females invested in reproduction and that all produced a single fawn. For males, we assumed that both subadult and adult males engaged in rutting (McTaggart Cowan 1956) and hence invested energy in reproduction. Table 1.1 summarizes the life history and demographic parameters used to assess the energy requirements of the local deer populations.

Table I.1: Life history and demographic parameters (obtained from camera-trap data and deer captures). Estimated abundances (N), female sex ratios (P_{female}), age ratios (μ) and body masses (W: mean \pm sd, number of individuals (n)) for each sex and age class (i.e.: female adult, male adult, female subadult, male subadult, fawn) in summer and winter, as well as the sex and age classes investing in reproduction are presented.

	East Limestone		Kunga	
ABUNDANCE				
N	36		168	
SEX RATIO				
P_{female}	0.68		0.51	
AGE RATIO in:	Summer	Winter	Summer	Winter
μ_{adult}	0.66	0.66	0.66	0.66
μ_{subadult}	0.34	0.19	0.34	0.17
μ_{fawn}	0	0.15	0	0.17
BODY MASS (kg) in:	Summer	Winter	Summer	Winter
$W_{\text{female.adult}}$	34 \pm 2 (n=6)	33 \pm 5 (n=3)	32 \pm 4 (n=7)	29 \pm 1 (n=4)
$W_{\text{male.adult}}$	43 \pm 12 (n=3)	36 \pm 6 (n=3)	42 \pm 10 (n=7)	38 \pm 4 (n=3)
$W_{\text{female.subadult}}$	26 \pm 6 (n=2)	23 \pm 3 (n=2)	25 \pm 5 (n=3)	21 \pm 4 (n=2)
$W_{\text{male.subadult}}$	24 \pm 3 (n=4)	24 \pm 3 (n=3)	26 \pm 2 (n=2)	25 \pm 4 (n=2)
W_{fawn}		18 \pm 3 (n=4)		14 \pm 3 (n=3)
REPRODUCTIVE INVESTMENT				
Invest	Adult females, adult males, subadult males			
Do not invest	Subadult females, fawns			

Table I.2: Metabolic parameters used in the deer model. For each sex and age-class (i.e.: female adult, male adult, female subadult, male subadult, fawn), for each season (i.e. summer and winter), and for each reproductive stage (i.e. maintenance and reproduction), the estimates of the seasonal proportion of day spent in a given stage (θ), the estimates of the proportion of day within the stage considered during which thermoregulation costs is considered (ω) and the Activity Metabolic Rate factor (AMR) of the stage considered are presented.

Sex	Age	Season	Stage	θ	ω	AMR
Female	Adult	Summer	Maintenance	0.33 ²	1	2 ¹
Female	Adult	Summer	Reproduction	0.67 ²	0.25	3.5 ²
Female	Adult	Winter	Maintenance	1	1	2 ¹
Female	Subadult	Summer	Maintenance	1	0.5	2 ¹
Female	Subadult	Winter	Maintenance	1	1	2 ¹
Male	Adult	Summer	Maintenance	1	0.5	2 ¹
Male	Adult	Winter	Reproduction	0.33 ¹	1	2.5 ¹
Male	Adult	Winter	Maintenance	0.67 ¹	1	2 ¹
Male	Subadult	Summer	Maintenance	1	0.5	2 ¹
Male	Subadult	Winter	Reproduction	0.33 ¹	1	2.5 ¹
Male	Subadult	Winter	Maintenance	0.67 ¹	1	2 ¹
Both	Fawn	Winter	Maintenance	1	1	2 ¹

¹Wallmo et al 1977

²Sadleir 1982 The activity metabolic rate factor of black tailed females with a single fawn was estimated to be 3.89 during the two first month of lactation, and to be 2.9 during the last two months of lactation. Thus, on average we estimate it to be 3.5 during the four month post parturition.

I.B.2.b. Estimation of energy required

To assess the energy requirements of the deer populations, we used Kleiber's equation (1947 in Robbins 1993, Parker et al. 1999) to estimate metabolic requirements from basal metabolic rate (BMR (kcal/day) = $70 \cdot W^{0.75}$, with W the body mass (kg) and 1 kcal = 4.1868 kJ), multiplied by an activity metabolic rate (AMR) factor. The basal metabolic rate represents the energy expenditure of an animal in a thermoneutral environment, in muscular and psychic repose and in a post-absorptive state (Kleiber et al. 1961 in Robbins 1993) and hence can be considered as a metabolic constant. The activity metabolic rate integrates any kind of additional metabolic activity and hence depends on season, sex, age and reproductive state (Robbins 1993). We calculated the population energy requirements for maintenance only and for both maintenance and reproduction by adjusting the AMR factor.

Values of the AMR factor (Table I.2) were obtained from Wallmo et al. (1977), Sadleir (1982) and Robbins (1993). We assumed that reproductive costs were significant for adult females when lactating (June to August) and for adult and subadult males during the early winter (rut season in October - November). We disregarded productive costs for antler growth and pelage molting because they represent less than 5% of the basal metabolic rate (Robbins 1993). Fawn weaning occurs between 2 and 4 months after parturition (Robbins 1993). Thus, to simplify we considered fawns as herbivores during the winter season only, disregarding their plant requirements in late summer.

In addition we also integrated thermoregulation costs with maintenance costs. Indeed, the thermal environment can be an important factor in deer energy requirements (Parker 1988). For example, on Channel Island (Alaska, U.S., 6° North of the study area), Parker et al. (1999) reported that black-tailed deer experienced a winter peak of thermal stress in February and a summer peak in June. In February, thermal stress occurred during c. 40% of weather observations and resulted in an additional metabolic cost for deer estimated to be 7% above the cost of standing (Parker et al. 1999, p.26). We estimated this cost to be equivalent to 15% of deer winter basal metabolic rate (BMR) (Parker et al. 1999: see definition of standing metabolic rate, p.13). In June, thermal stress occurred during c. 50% of the observation and increased

energy cost of standing by < 6% (i.e. < 13% of deer summer BMR, Parker et al. 1999, p.13 and 29). Air temperature, rain and wind are the main factor affecting deer thermal balance (Parker 1988). During their study period, Parker et al. (1999, p.10) recorded mean minimum air temperatures in winter and summer > -3°C and > 6°C, respectively, with important rainfall > 290 mm in November and > 100 mm during the summer. Snow is also common on Channel Island with snow depth exceeding 80 cm in some areas. In comparison, our study area presents overall milder climatic characteristics with average minimum daily temperature > 0°C in winter and > 6°C in summer (except in April when the average minimum and maximum daily temperature were c. 3 °C and 10°C), average monthly rainfall < 200 mm in winter and < 100 mm in summer, and snow depth < 3cm (Sandspit weather station: Environment Canada data). Deer at our study sites are thus likely to experience lower thermal stress than deer on Channel Island, even in April when the effect of lower temperatures may be buffered by a gradual spring pelage molt (April to late June in black-tailed deer on Vancouver Island, Canada, 2° South of the study area; McTaggart Cowan & Raddi 1972). To be conservative we considered that deer would experience thermal stress from October to June with an additional daily cost equal to 15% of deer BMR. As the average snow depth recorded at the Sandspit weather station always fell below the 30-cm and 55-cm thresholds beyond which additional locomotion costs should be added to black-tailed deer energy requirements (Parker et al. 1984), we did not consider extra locomotion costs in our model.

For each season we estimated the energy requirements of deer populations by summing over sex and age classes the energy requirement of each class multiplied by the sex and age ratios of the class and by the deer population abundance.

Based on the above description we calculated the seasonal maintenance energy requirements (MER) of the deer population of each island according to Equation 2.

$$MER = N \cdot nd_{season} \left[\sum_{sex} \rho_{sex} \left[\sum_{age} \mu_{age,season} \left((AMR_{a..x.s} + 0.15 \cdot \omega_{season}) \cdot BMR_{a..x.s} \right) \right] \right]$$

(Equation 2)

where N is the local deer abundance, nd_{season} is the number of days of the season considered (i.e. 183 days in summer and 182.25 days in winter), ρ_{sex} is the sex ratio of the sex considered, $\mu_{age.season}$ is the age ratio of the age considered during a given season, ω_{season} is the within-season proportion of days during which a thermoregulation cost of 0.15 BMR is integrated to deer maintenance costs (i.e. 0.5 in summer (thermoregulation costs from April to June) and 1 in winter (thermoregulation costs from October to March)), $AMR_{a,x,s}$ is the Activity Metabolic Rate factor for maintenance of the class of age a and sex x considered during the season s , and $BMR_{a,x,s}$ is the Basal Metabolic Rate of the class of age a and sex x during the season s , considered to be equivalent to $70 \cdot W_{a,x,s}^{0.75}$ with $W_{a,x,s}$ being the average deer body mass of the class of age a and sex x during the season s .

Similarly, the seasonal energy requirements of the local deer population including reproductive costs (RER) were computed for each island by adding reproduction-related parameters to Equation 2 (Equation 3).

$$RER = N \cdot nd_{season} \left[\sum_{sex} \rho_{sex} \left[\sum_{age} \mu_{age.season} \left[\sum_{stage} \beta_{stage} \cdot (AMR_{stage.a.x.s} + 0.15 \cdot \omega_{stage.a.x.s}) \cdot BMR_{a.x.s} \right] \right] \right]$$

(Equation 3)

where β_{stage} is the proportion of days of the season s during which the class of sex x and age a is in a given reproductive stage, $AMR_{stage.a.x.s}$ is the Activity Metabolic Rate factor of the stage for the class of age a and sex x during the season s and $\omega_{stage.a.x.s}$ is the proportion of days of the reproductive stage during which a thermal cost is integrated to maintenance costs for the class of age a and sex x during the season s).

I.C. ANALYSIS

For each island, we compared the estimates of the energy available from the vegetation with the energy required by the deer population by assessing the proportion of deer maintenance energy requirements met by each resource for each season and for each habitat scenario (i.e. in the absence or presence of windfall). To compare the energy requirements including reproductive costs with the energy resources available, we assessed the proportion of energy required by the deer model including reproductive costs (Equation 3) as a function of the energy

required as estimated by the model including maintenance costs only (Equation 2) and compared it with the proportions calculated for the energy resources. Reproduction costs increased deer energy requirements on East Limestone and Kunga islands, respectively, by 22 and 16% in summer and 2 and 4 % in winter.

To account for variability in the three main parameters measured in the field (i.e. available dry biomass, deer population density and body mass), we conducted 5,000 simulations for both models (i.e. resource and deer models) where these parameters were randomly generated from normal distributions calibrated on their means and their standard deviations. To be conservative, for body mass, we used for each island a single standard deviation value per age class, estimated to be the higher values assessed for the given age class on both sexes during both seasons (SM.I.2). We compared the average and the 95% confidence interval of the energy available to and required by East Limestone and Kunga deer populations for each habitat scenario (i.e. in the absence or presence of windfall). The results from the simulation models were consistent with those obtained from the model run with the average field values. Here we present the results assessed with the average values measured in the field only and the simulation analysis is detailed as supplementary information (SM.I.2).

II. RESULTS

II.A. ENERGY AVAILABLE VS. ENERGY REQUIRED

In the absence of windfall (Figure I.1), we estimated the energy available in summer to exceed the energy required by deer populations on both islands. On East Limestone, the energy available to the local deer population covered 178% of their energy requirements when we did not include reproductive costs and 146% when we included these costs (see Figure I.1 A). On Kunga we estimated these values to be 375 and 323%, respectively (see Figure I.1 C). In winter the energy available met c. 25 and 50% of the energy required by East Limestone and Kunga deer populations, respectively (see Figure I.1 B,D).

Under the habitat scenario that included windfall areas (Figure I.2), we estimated the energy available to the deer population on East Limestone in summer to cover 138% of the deer energy

requirements when we did not include reproductive costs and 113% when we included these costs (see Figure 1.2 A). On Kunga we estimated these values to be 325 and 280%, respectively (see Figure 1.2 C). In winter we estimated the energy available to deer to meet c. 30 and 60% of their energy requirements on East Limestone and Kunga islands, respectively (see Figure 1.2 B,D).

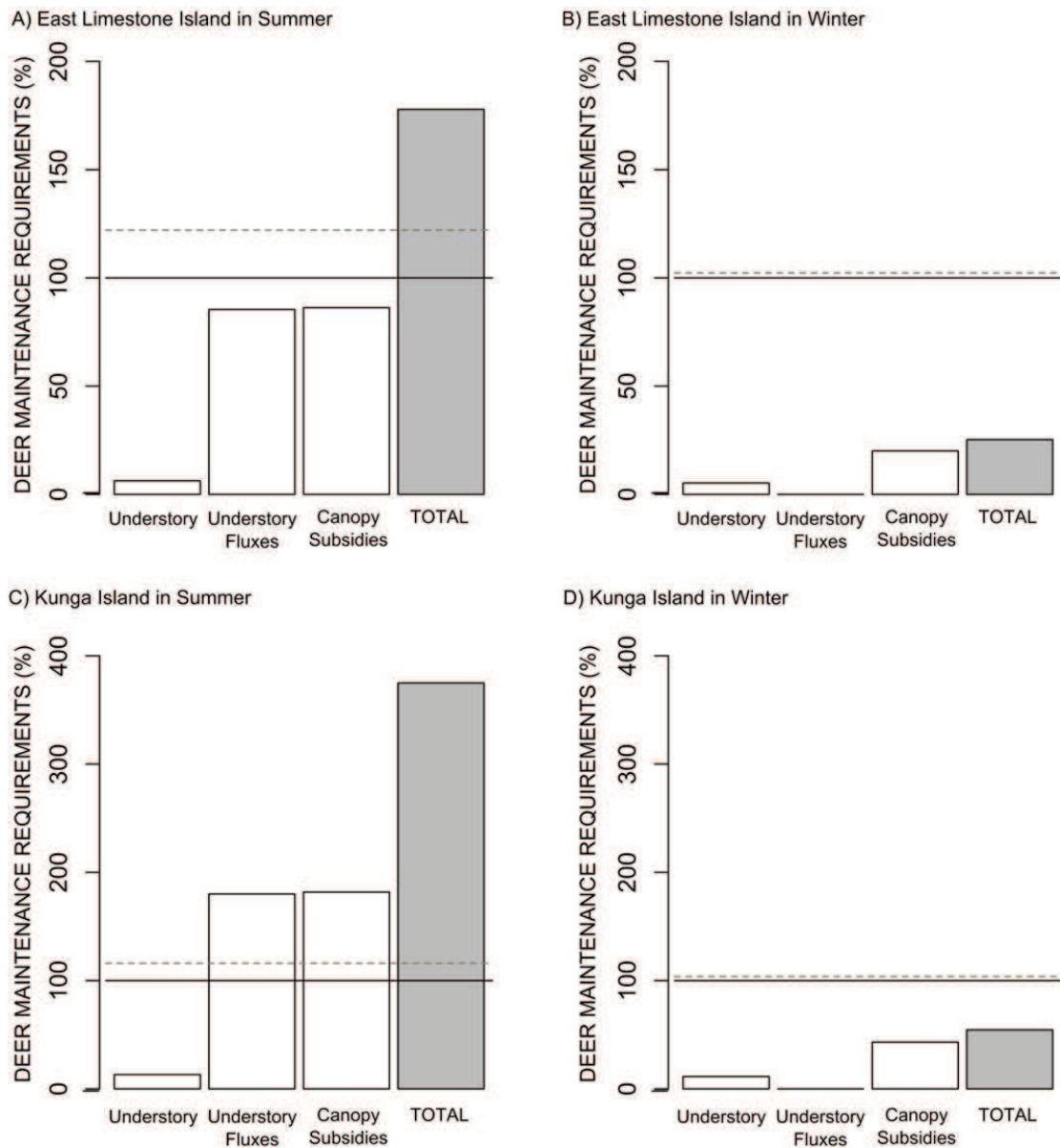


Figure I.1: Estimated energy balances on East Limestone (A, B) and Kunga islands (C, D) under the scenario not accounting for windfall areas. Open bars give the percentage of the deer maintenance energy requirements (i.e. energy needed to maintain the studied deer populations without accounting for reproductive costs) that are covered by the energy available from each type of resource (i.e. understory, understory fluxes and canopy subsidies). The grey bars give the sum of the white bar values (i.e. the total percentage of the maintenance energy requirements of the deer population covered by all resources available). The solid lines refer to the level of energy needed to maintain the deer populations without accounting for reproductive costs (100%). The dashed lines refer to the energy requirements of the deer populations when accounting for reproductive costs (i.e. on East Limestone 122% in summer (April–September) and 102% in winter (October–March), and on Kunga 116% in summer and 104% in winter).

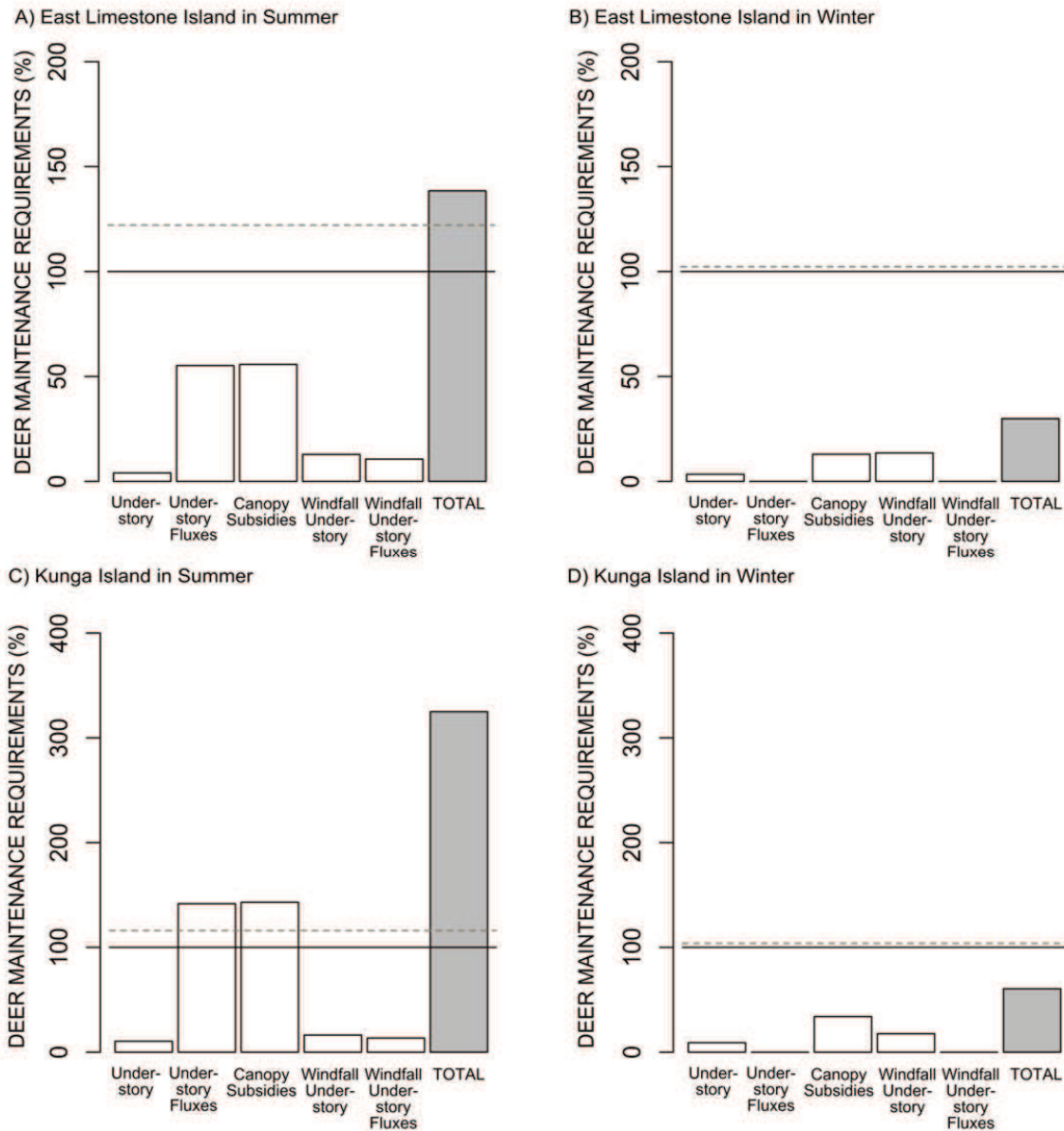


Figure I.2: Estimated energy balances on East Limestone (A, B) and Kunga islands (C, D) under the scenario accounting for windfall areas. Open bars give the percentage of the deer maintenance energy requirements (i.e. energy needed to maintain the studied deer populations without accounting for reproductive costs) that are covered by the energy available from each type of resource (i.e. understory, understory fluxes and canopy subsidies in forest areas and understory and understory fluxes in windfall areas). The grey bars give the sum of the white bar values (i.e. the total percentage of the maintenance energy requirements of the deer population covered by all resources available). The solid lines refer to the level of energy needed to maintain the deer populations without accounting for reproductive costs (100%). The dashed lines refer to the energy requirements of the deer populations when accounting for reproductive costs (i.e. on East Limestone 122% in summer (April-September) and 102% in winter (October-March), and on Kunga 116% in summer and 104% in winter).

II.B. WHAT COMPONENT OF THE VEGETATION CONTRIBUTES TO MAINTAINING THE DEER POPULATIONS?

In the absence of windfall (see Figure I.1), the understory biomass met respectively c. 5 and 11% of the energy requirements of East Limestone and Kunga deer populations whatever the season. In summer, understory fluxes and canopy subsidies each met c. 70% of the energy requirements including reproductive costs of the East Limestone deer population and more than 150% of the energy requirements including reproductive costs of the Kunga deer population. In winter the canopy subsidies met c. 20 and 40% of the energy requirements of the deer populations on East Limestone and Kunga islands, respectively.

Under the habitat scenario that included windfall (see Figure I.2), the contribution of understory fluxes and canopy subsidies to the summer energy requirements of the East Limestone population, including reproduction costs, decreased from 70 to 54% and from 71 to 46%, respectively. These values varied from 155 to 134% and from 157 to 123% for the Kunga population, respectively. In winter the contribution of the canopy subsidies to the energy requirements of East Limestone and Kunga populations, including reproductive costs, decreased to 7 and 9%, respectively. However, the presence of windfall areas increased the proportion of the deer energy requirements met by the understory of c. 10-15% on both islands for both seasons.

For both habitats (i.e. forest and windfall areas, respectively) the energy provided by the understory fluxes came primarily from perennial rhizomatous grasses (81% and 66%, respectively), forbs (19% and 2%, respectively) and shrubs (<1% and 30%, respectively) (see Table I.3). In forest areas, red alder provided 90% of the energy provided by the canopy subsidies in summer and 54% in early winter; red cedar and lichen provided the remaining energy available in late winter (i.e. 42 and 4%).

Table I.3: Specific contributions to the dry biomass and to the seasonal available energy of the two main resources: understory fluxes and canopy subsidies.

Species	Percentage of dry biomass (%)	Reproduction and/or production structures	Guild	Percentage of energy available in summer within a resource (%)	Percentage of energy available in winter within a resource (%)
UNDERSTORY FLUXES					
FOREST AREAS					
<i>Carex sp.</i>	42.04	rhizome	grass	44.08	no flux
<i>Calamagrostis nutkaensis</i>	31.89	rhizome	grass	29.59	no flux
<i>Stellaria crispa</i>	14.43	rhizome	forb	14.74	no flux
<i>Luzula parviflora</i>	7.18	rhizome	grass	7.04	no flux
<i>Galium sp.</i>	2.15	rhizome	forb	2.19	no flux
<i>Cardamine oligosperma</i>	1.75	rhizome	forb	1.78	no flux
<i>Athyrium filix-femina</i>	0.18	rhizome - propagule	fern	0.19	no flux
<i>Vaccinium parvifolium</i>	0.17	rhizome	shrub	0.18	no flux
<i>Listera sp.</i>	0.15	rhizome	forb	0.17	no flux
<i>Tsuga heterophylla</i>	0.06	seed	tree	0.03	no flux
<i>Moneses uniflora</i>	0.00	rhizome	forb	0.00	no flux
<i>Picea sitchensis</i>	0.00	seed	tree	0.00	no flux
WINDFALL AREAS					
<i>Luzula parviflora</i>	44.48	rhizome	grass	42.72	no flux
<i>Vaccinium parvifolium</i>	29.15	rhizome	shrub	30.48	no flux
<i>Bromus sp.</i>	21.56	rhizome	grass	23.10	no flux
<i>Tsuga heterophylla</i>	1.47	seed	tree	0.73	no flux
<i>Maianthemum dilatatum</i>	1.33	rhizome - seed	forb	1.53	no flux
<i>Picea sitchensis</i>	1.17	seed	tree	0.59	no flux
<i>Moneses uniflora</i>	0.62	rhizome	forb	0.65	no flux
<i>Calamagrostis nutkaensis</i>	0.22	rhizome	grass	0.20	no flux
CANOPY SUBSIDIES					
FOREST AREAS					
<i>Alnus rubra</i>	77.40	canopy tree	tree	90.06	53.57
<i>Thuja plicata</i>	21.16	canopy tree	tree	9.00	42.35
<i>Lichen sp.</i>	1.44	canopy tree	lichen	0.94	4.08

III. DISCUSSION

Despite the dramatic reduction in understory vegetation resulting from decades of unrestricted browsing (Stockton et al. 2005, Martin et al. 2010, Chollet et al. 2013) our results suggest that food resources in summer are adequate, accounting for the successful reproduction observed in most adult females. Energy needs are met principally through understory fluxes and canopy subsidies, two food sources that are relatively cryptic to the casual observer. Kunga, especially, was estimated to provide three times more energy than required to maintain the local population, although some uncertainty is created by the large confidence limits on our population estimate.

However, our results also indicate that black-tailed deer on our study sites suffered an overall energy deficit during the winter period. The ability of deer to persist in situations where food is abundant in summer but insufficient in winter has been well documented (Moen 1976, Wallmo et al. 1977, Parker et al. 1996, 1999). Over-winter survival is achieved by the use of body reserves built up during summer, as shown by Parker et al. (1999) in Sitka black-tailed deer and by Mautz (1978) and Huot (1982) in white-tailed deer. This is consistent with the 9% average body mass gain observed in 8 adult deer we captured in March-April and recaptured in August-October of the same year.

Despite assumptions and uncertainties in estimating the amounts of energy available and energy required by the deer populations, our results are qualitatively robust and the overall pattern observed stands up to variations of many model parameters. Numerical results particularly depend on the three main parameters we estimated in the field (i.e. specific dry biomass, deer body mass and deer density). To better assess this variability we simulated 5,000 sets of these parameters within the ranges observed. In spite of the high levels of variability in deer body mass (sd: 6 - 12 kg) or in deer density (sd: 10–31 deer/km²) considered, we obtained similar results (i.e. a positive summer balance) for 84% and 97% of simulations for East Limestone and Kunga deer energy balance, respectively, supporting the overall pattern described (SM.I.2). Further studies, especially multi-year surveys of resource availability and deer demography would (i) improve the accuracy and scope of our quantitative results and (ii)

document inter-annual variation in deer energy balance and in the relative contribution of each pool of resources to the maintenance of these populations. Nevertheless, despite current uncertainties, the present work can be considered as a qualitative modeling exercise highlighting the remarkable potential of a heavily browsed environment to support dense deer populations via understory fluxes and canopy subsidies.

For simplicity, we did not consider spatial heterogeneity in food access and distribution, nor the ability and preferences of deer to find, handle, ingest and digest each type of resource. Such behavioral and physiological constraints may be critical in the response of plants to herbivory (Power 1992) and in the efficiency with which deer can use the resources available (Robbins 1993). This might affect the spatio-temporal dynamics in resource use by deer, but likely not the overall pattern observed.

Resources not included in our study may also participate in maintaining the local deer populations. Similar to Scottish red deer (*Cervus elaphus*) on the Isle of Rum that use seaweed as a food supply (Conradt 2000), our direct observations and fecal micro-histological analyses (E. Poilvé pers. comm.) support the use of brown and red algae in the winter and summer diet of East Limestone and Kunga deer. Given that brown seaweeds such as *Alaria* sp have an energy value of about 10 kJ/g dry matter (Applegate & Gray 1995) similar to that of ferns (see Appendix I.A), seaweed may be a non-negligible energy resource for deer, especially in winter.

Interestingly the results obtained for the scenario including windfall highlighted the importance of canopy subsidies and understory fluxes as food supplies. Despite the loss of more than 20% of forest area and its associated canopy subsidies, on both islands the remaining forested area and its canopy subsidies accounted for more than 40% of the energy available to deer during both winter and summer and covered more than half of the summer maintenance energy requirements of the local deer populations, supporting the studies by Rochelle (1980), Takahashi & Kaji (2001) and Tremblay et al. (2005) that highlighted the potential of canopy windfalls as a food supply for deer. In addition, windfall areas by themselves covered about 20% of the energy requirement of the reproductive deer population on both islands, via understory

fluxes (c. 9-12%) and via an extra food supply in the understory layer (c. 11-14%) provided by the temporary access to the crown foliage of the fallen trees.

Because the consumption of canopy subsidies (leaves and twigs of red alder and redcedar, especially) does not directly affect the growth, survival or reproduction of the resource-producer plants (i.e. tall canopy trees), there is no feedback effect of the deer on canopy subsidies, except possibly indirectly through changes in soil quality (e.g. soil structure, texture, and composition: Bardgett & Wardle 2003). This was reported in Isle Royal National Park where moose browsing decreased soil fertility (Pastor et al. 1993). Understory fluxes resulted mostly from perennial rhizomatous plant species tolerant of herbivory and to a lesser extent from tree seedlings germinating from the seed bank (see Table I.3). By definition, herbivory has a low impact on the survivorship of tolerant plant species (Augustine & McNaughton 1998) and hence a low impact on the availability of the resource. Similarly the persistence of the seed bank depends on the productivity and fertility of plants that grow above browsing height or in refuges inaccessible to deer (Chollet et al. 2013). The seed bank subsidies may be affected by herbivory via changes in future recruitment and/or in biomass productivity and fertility rates (Louda et al. 1990, Abbas et al. 2012), but such changes would happen only in the long term. Thus, currently both canopy subsidies and understory fluxes are only weakly linked to resource consumption. Consequently they help to mitigate the effects of high herbivory on deer population density.

Our approach, though simplified, provides qualitative support for the existence of processes that may delay resource-driven feedback on herbivore populations. Such a delay may be particularly critical to consider when herbivores occur in predator-free environments where costs associated with vigilance or habitat shifts are reduced and/or in mild environments where climate-controlled population dynamics are unlikely. Within the current framework of worldwide increases in temperate forest herbivore populations, managers should be aware of the existence of potential delays in the control of herbivores via resource-driven feedback processes and hence may have to consider other processes including “top-down” control to achieve their management goals of limiting herbivore populations before dramatic changes in vegetation occur. Indeed, whereas a strategy for herbivore management may be the “laisser-

faire” that claims that a natural area left alone will reach a notional “wilderness equilibrium” (Gordon & Prins 2008), here we highlighted that such equilibrium may be far different from the current forest state, as herbivore abundance may continue to be high right up to the point where the canopy begins to disappear.

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APPENDIX I.A

Parameters used in the resource model: For each plant species inventoried as a resource we recorded for each season (i.e. summer and winter) its seasonal availability (number of days available in the season), its digestible energy content (kJ / g Dry Matter), the species and season considered in the published data used and the publication.

Guild	Family	Species Latin name	summer availability (nb days)	winter availability (nb days)	Digestible Energy (kJ/gDM) - summer	Digestible Energy (kJ/gDM) - winter	species with published energetic values when not the same	period of published summer data	period of published winter data	Source of summer data	Source of winter data
Tree	Betulaceae	<i>Alnus rubra</i>	183	31	13.6899	10.1739	same (leaves, buds, catkins)	summer	oct 77	Hanley et al.2012	Seip 1979
		<i>Aquilegia formosa</i>	122	31	11.9498	11.9498	same	summer	summer	Hanley et al.2012	Hanley et al.2012
Fern	Woodsiaceae	<i>Athyrium filix-femina</i>	183	182.25	12.0357	12.0357	same (leaves, fiddleheads)	apr-jun-aug-sept 89- apr-may-aug 90	apr-jun-aug-sept 89- apr-may-aug 90	Parker et al. 1999	Parker et al. 1999
Fern	Blechnaceae	<i>Blechnum spicant</i>	183	182.25	9.4240	11.6233	same	apr-aug-sep 89- jun-aug 90	oct 88-dec 89-mar 90	Parker et al. 1999	Parker et al. 1999
Grass	Poaceae	<i>Bromus sp.</i>	183	182.25	12.8082	12.8082	<i>Poacea (Elymus arenarius, Deschampsia caespitosa, Hordeum brachyantherum)</i>	apr-sept89-mar-aug90	apr-sept89-mar-aug90	Parker et al. 1999	Parker et al. 1999
Grass	Poaceae	<i>Calamagrostis nutkaensis</i>	183	182.25	10.8548	10.8548	<i>Graminoids</i>	summer	summer	Hanley et al.2012	Hanley et al.2012
		<i>Calypso bulbosa</i>	122	31	13.5530	13.5530	<i>Listera sp</i>	summer	summer	Hanley et al.2012	Hanley et al.2012
Forb	Orchidaceae	<i>Campanula rotundifolia</i>	122	31	11.9498	11.9498	other forbs	summer	summer	Hanley et al.2012	Hanley et al.2012
Forb	Brassicaceae	<i>Cardamine oligosperma</i>	122	31	11.9498	11.9498	other forbs	summer	summer	Hanley et al.2012	Hanley et al.2012
Grass	Cyperaceae	<i>Carex sitchensis</i>	183	182.25	12.2675	11.6800	<i>Carex sp.</i>	apr-jun 89-may-jun90	dec 88-mar-90	Parker et al. 1999	Parker et al. 1999
Forb	Asteraceae	<i>Cirsium sp.</i>	183	182.25	13.0863	13.0863	<i>Asteraceae (Prenanthes alata, Achillea millefolium)</i>	may-aug-sept89- jun-aug 90	may-aug-sept89- jun-aug 90	Parker et al. 1999	Parker et al. 1999
		<i>Conioselinum pacificum</i>	153	31	13.1300	13.1300	same	jun-sept 89- jun 90	jun-sept 89- jun 90	Parker et al. 1999	Parker et al. 1999
Fern	Dryopteridaceae	<i>Dryopteris expansa</i>	183	182.25	10.5224	7.7851	same	summer	winter	Hanley et al.2012	Hanley et al.2012
Fern	Pteridophyte	<i>Fern sp.</i>	183	182.25	10.7461	10.5907	<i>Fern (Athyrium filix-femina (leaves, fiddleheads), Blechnum spicant, Dryopteris dilatata (leaves, rhizomes, fiddleheads), Polypodium vulgare, Polystichum Braunii)</i>	summer- apr-jun-aug-sep	winter-mar- apr-jun-aug-sep	Parker et al. 1999,	Parker et al. 1999,
		<i>Fern sp.</i>	183	182.25	10.7461	10.5907	<i>Poacea (Elymus arenarius, Deschampsia caespitosa, Hordeum brachyantherum)</i>	89- apr-may- jun-aug 90	89- apr-may- aug-mar-dec 90	Hanley et al.2012	Hanley et al.2012
Grass	Poaceae	<i>Festuca rubra</i>	183	182.25	12.6953	13.2600	<i>Poacea (Elymus arenarius, Deschampsia caespitosa, Hordeum brachyantherum)</i>	apr-sep 89-aug 90	mar 90	Parker et al. 1999	Parker et al. 1999
Forb	Rubiaceae	<i>Galium aparine</i>	122	31	11.9498	11.9498	<i>Galium sp</i>	summer	summer	Hanley et al.2012	Hanley et al.2012
Forb	Rubiaceae	<i>Galium triflorum</i>	122	31	11.9498	11.9498	<i>Galium sp</i>	summer	summer	Hanley et al.2012	Hanley et al.2012
Shrub	Ericaceae	<i>Gaultheria shallon</i>	183	182.25	5.7419	5.7419	same (leaves, twigs)	summer	winter	Hanley et al.2012	Hanley et al.2012

Appendix I.A (continued)

Guild	Family	Species Latin name	summer availability (nb days)		winter availability (nb days)	Digestible Energy (kJ/gDM) -		species with published energetic values when not the same	period of published summer data	period of published winter data	Source of summer data	Source of winter data
			summer	winter		summer	winter					
Lichen	Lichen	<i>Lichen sp.</i>	183	182.25	13.3966	12.4000	<i>Lichen (Alectoria sp, Usnea sp, Lobaria sp, Conocephalum conicum)</i>	summer	oct-dec-88-mar-sept-dec 89-mar 90		Hanley et al.2012	Parker et al. 1999
Forb	Orchidaceae	<i>Listera caurina</i>	122	31	13.5530	13.5530	<i>Listera sp</i>	summer	summer	summer	Hanley et al.2012	Hanley et al.2012
Forb	Orchidaceae	<i>Listera cordata</i>	122	31	13.5530	13.5530	same	summer	summer	summer	Hanley et al.2012	Hanley et al.2012
Forb	Orchidaceae	<i>Listera sp.</i>	122	31	13.5530	13.5530	<i>Listera sp</i>	summer	summer	summer	Hanley et al.2012	Hanley et al.2012
Shrub	Caprifoliaceae	<i>Lonicera involucrata</i>	183	182.25	18.5301	11.8696	<i>Lonicera japonica (leaves & twig)</i>	apr-may-jun-jul-aug-sept	dec	dec	Munger 2002	Munger 2002
Grass	Juncaceae	<i>Luzula parviflora</i>	183	182.25	11.4805	11.4805	same	summer	summer	summer	Hanley et al.2012	Hanley et al.2012
Forb	Ruscaceae	<i>Maianthemum dilatatum</i>	122	31	13.7840	13.7840	same	may-aug-sept	may-aug-sept	may-aug-sept	Parker et al. 1999	Parker et al. 1999
Tree	Rosaceae	<i>Malus fusca</i>	183	31	14.0060	14.0060	same	may-aug-sept 89-jun-aug 90	may-aug-sept 89-jun-aug 90	may-aug-sept 89-jun-aug 90	Parker et al. 1999	Parker et al. 1999
Shrub	Ericaceae	<i>Menziesia ferruginea</i>	183	182.25	10.6940	6.4200	same (leaves & stem)	jun-aug-sep 89-may-aug 90	oct 88	oct 88	Parker et al. 1999	Parker et al. 1999
Forb	Ericaceae	<i>Moneses uniflora</i>	122	31	12.3995	12.0280	same	summer	winter	winter	Hanley et al.2012	Hanley et al.2012
Tree	Pinaceae	<i>Picea sitchensis</i>	183	182.25	5.9667	5.2237	same	summer	winter	winter	Hanley et al.2012	Hanley et al.2012
Tree	Coniferous	<i>Picea sitchensis, Tsuga het.</i>	183	182.25	5.9667	5.2237	same	summer	winter	winter	Hanley et al.2012	Hanley et al.2012
Fern	Polypodiaceae	<i>Polypodium glycyrrhiza</i>	183	151.25	11.4800	12.8833	<i>Polypodium vulgare</i>	sept-89-aug 90	mar-dec 89-90	mar-dec 89-90	Parker et al. 1999	Parker et al. 1999
Fern	Polytrichaceae	<i>Polystichum munitum</i>	183	151.25	10.2683	8.6259	<i>Polystichum Braunii</i>	summer	winter	winter	Hanley et al.2012	Hanley et al.2012
Forb	Asteraceae	<i>Prenanthes alata</i>	122	31	13.3100	13.3100	same	may-aug-sept 89-may-aug 90	may-aug-sept 89-may-aug 90	may-aug-sept 89-may-aug 90	Parker et al. 1999	Parker et al. 1999
Shrub	Grossulariaceae	<i>Ribes lacustre</i>	183	182.25	8.6943	5.3215	<i>Ribes sp (leaves & twig)</i>	summer	winter	winter	Hanley et al.2012	Hanley et al.2012
Shrub	Rosaceae	<i>Rubus spectabilis</i>	183	31	13.1650	9.5961	same	may 89-jun 90	oct 77	oct 77	Parker et al. 1999	Selp 1979
Shrub	Ericaceae	<i>Sambucus racemosa ssp. p.</i>	183	31	9.8674	9.8674	same (leaves, twigs)	summer	summer	summer	Hanley et al.2012	Hanley et al.2012
Forb	Caryophyllaceae	<i>Stellaria crispa</i>	122	31	11.9498	11.9498	same	summer	summer	summer	Hanley et al.2012	Hanley et al.2012
Tree	Cupressaceae	<i>Thuja plicata</i>	183	182.25	8.5867	8.5867	same	summer	winter	winter	Hanley et al.2012	Hanley et al.2012
Tree	Pinaceae	<i>Tsuga heterophylla</i>	183	182.25	5.9667	5.2237	same	summer	winter	winter	Hanley et al.2012	Hanley et al.2012
Shrub	Ericaceae	<i>Vaccinium parvifolium</i>	183	182.25	12.5000	10.1740	same (leaves, twigs)	mar-may-sept 89-apr-may-aug 90	oct 88-mar-dec 89-mar 90	oct 88-mar-dec 89-mar 90	Parker et al. 1999	Parker et al. 1999

SUPPLEMENTARY MATERIALS

SM.I.1: DEER ABUNDANCE ESTIMATION BY CAPTURE MARK RECAPTURE METHODS

I. MATERIAL & METHODS

I.A. EXPERIMENTAL DESIGN

We estimated deer abundance on East Limestone and Kunga via a capture-mark-recapture (CMR) method using camera trap data. This survey used motion sensor cameras (RECONYX PC 900) located along deer trails and set up to acquire a picture per second during 25 seconds each time an animal triggered the motion sensor. On each picture individuals were aged, sexed and identified when possible. To avoid misidentification biases, we used only pictures with clearly identified unmarked or marked individuals as suggested by Chandler & Royle (2013) (i.e. 91% of deer visits; Table SM.I.1.1).

We used Chandler & Royle's (2013) spatially-explicit CMR models to assess the local deer abundance. This method was selected because it allowed including marked and unmarked individuals. It involved both capture-recapture data (i.e. the total number of captures at each site on each capture occasion, the number of captures at each sites on each capture occasion for each marked individual) and spatial data (i.e., the camera location, the surface of the area surveyed, and deer activity center). We present here only the specificities of our experimental design, as well as the parameters used in Chandler & Royle's model. For a detailed presentation of the computation code, see the supplementary materials published with Chandler & Royle's study.

We defined a capture as a sequence of pictures starting with the arrival of an individual in the camera's field and finishing when the animal left the camera's field. We defined an "occasion" as a day of active camera. We defined a "site" as the location where a camera was set. We defined the "surveyed area" as the area used by individuals with a probability >0 to be detected at least at one site. We estimated deer annual home ranges for 15 does equipped with GPS collars on East Limestone and Kunga between April 2011 and June 2012 to range from 15 to 130

ha (unpublished data). This supported Bunnell's (1990 in Engelstoft 2007) results who reported an annual home range of 140 ha for resident black tailed deer on Vancouver Island (B.C., Canada). As a consequence, we defined the surveyed area as the intersection between a 650 meter - buffer area around the sites (i.e. a 133-ha buffer around each site) and the island area. Spatial computations were conducted with GIS systems using Gowgaia spatial data basis for island outlines (The Gowgaia Institute). We defined deer activity center for marked individuals as the barycenter of the sites where the individual was detected weighted by the number of visits spaced by more than 1 hour at a given site.

On East Limestone we surveyed six sites during 40 days with a surveyed area covering the whole island (Table SM.I.1.1). On Kunga, given the limited amount of cameras available and the large area to cover (395 ha), we conducted four sessions (i.e. sequences of consecutive days with the area surveyed kept constant) of four to six days spent surveying simultaneously six to nine sites that covered between 40 and 61 % of the island. The total area surveyed during the four sessions covered the whole island (see Table SM.I.1.1).

Table SM.I.1.1. Experimental design used to collect Capture-Mark-Recapture data

	East Limestone	Kunga- session 1	Kunga- session 2	Kunga- session 3	Kunga- session 4
Number of sites	6	9	7	6	7
Number of occasions	40	4	6	4	4
Area covered (ha)	41	214	309	348	301
Total number of marked individuals	17	18	18	18	18
Number of marked individuals detected on pictures	13	3	1	1	1
Total number of visits	218	19	29	12	43
Total number of visits by marked individuals	110	5	1	1	3

I.B. MODEL PARAMETERS

To estimate deer abundances for East Limestone and for each session surveyed on Kunga, we used Markov chain Monte Carlo (MCMC) simulations, more specifically 3 chains each consisting of 30,000 iterations. The model parameters used as priors are summarized in Table SM.I.1.2, with M being the maximum abundance value accepted in the model, σ a scale parameter determining the rate of decay in encounter probability, λ_0 the encounter rate for a null distance between an activity center and a camera site and ϕ the parameter of data augmentation (see Chandler & Royle 2013 for further details). We checked that acceptance rate of the MCMC algorithm lied between 40 and 60 %. We confined σ between 80 and 300 meters (Royle et al.'s 2011). We fixed the maximum abundance on East Limestone to 100 individuals and to 400 individuals for each session on Kunga.

Table SM.I.1.2: Prior values used to estimate deer abundance on East Limestone (ELI) and Kunga

	M	σ	λ_0	ϕ	Tune for σ	Tune for λ_0	Tune for S
ELI	100	[80 – 300]	[0.05 – 1]	[0 – 1]	30	0.1	150
Kunga	400	[80 – 300]	[0.05 – 1]	[0 – 1]	30	0.1	500

I.C. ABUNDANCE ESTIMATION

We discarded the initial 5,000 draws (burn-in period) and pooled the three simulated 25,000 last draws to estimate the 95% confidence interval on the deer abundance of the surveyed area and used the posterior mean of abundance in the deer model.

For Kunga, we had planned to estimate deer abundance by considering that the four sessions were temporally independent but slightly overlapping spatially. Thus, for each session we could estimate the density of the surveyed area and computed the deer abundance on the island as the union of the abundance estimated over the 4 sessions. That is to say, if we considered two sessions that surveyed two areas A and B and overlapped in a section $A \cap B$ (Figure SM.I.1.1) and

noted d_A and d_B the density estimated in A and B and d the average density between d_A and d_B , then $A \cdot d_A$ is the abundance in the area A, $B \cdot d_B$ is the abundance in the area B and the abundance of the union between A and B is $A \cdot d_A + B \cdot d_B - A \cap B (d_A + d_B) + A \cap B \cdot d$. The initial idea was to use this formula generalized for the union between 4 elements.

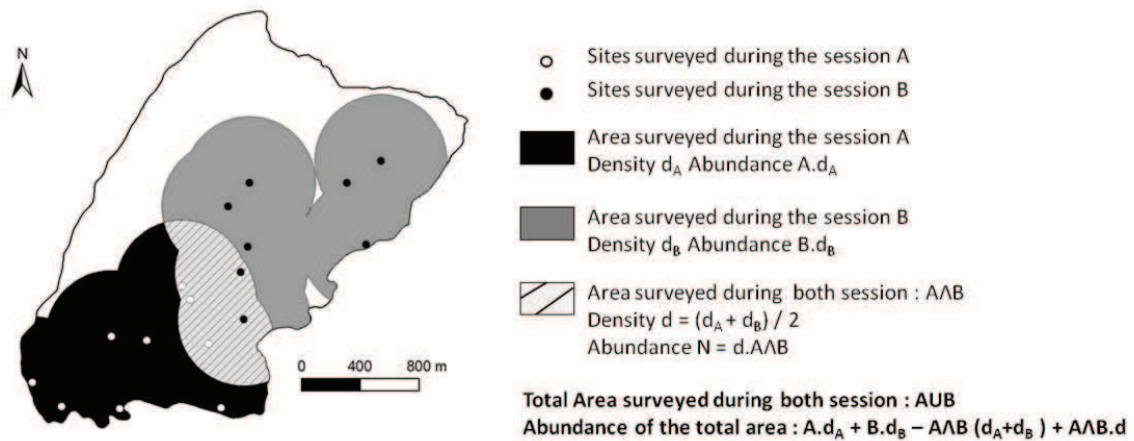


Figure SM.I.1.1: Method to estimate the abundance on Kunga: Example of the computation when 2 sessions are considered

However the model did not converge for three sessions on Kunga due to a sampling effort which was too low in relation to the deer visit frequency and the proportion of marked individuals. This generated a large range of possible parameter sets that hence did not converge (Figure SM.I.1.2 C-E). As a consequence we assumed that deer density was homogeneous over the island and estimated the island deer density as the deer density of the unique session for which the model converged (see Figure SM.I.1.2 B).

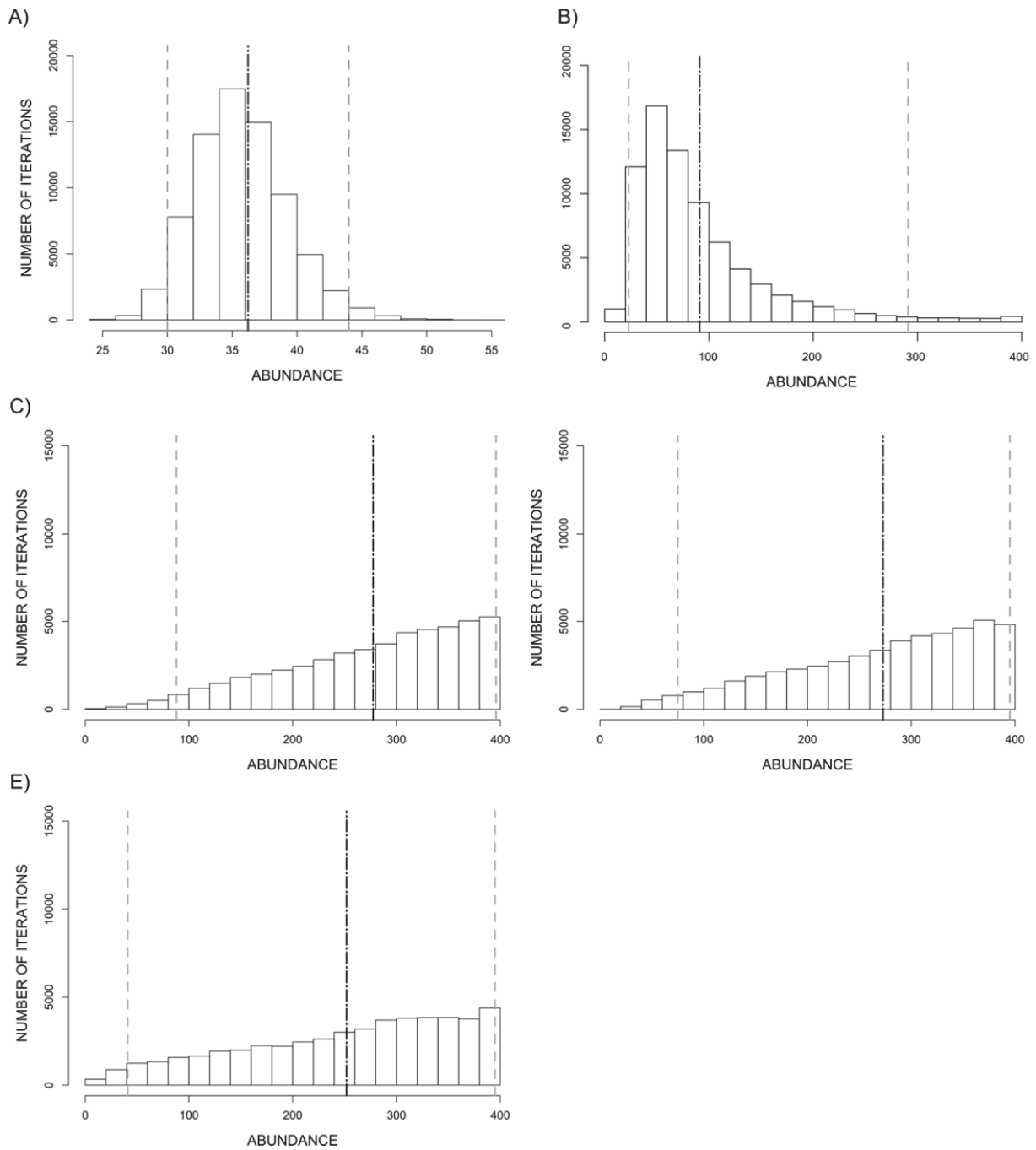


Figure SM.I.1.2: Distribution of deer abundance estimated on East Limestone (A), and Kunga for the four sessions considered (B,C,D,E). The number of iterations considered in the analysis (i.e. the last 25,000 iterations among the 30,000 simulated) (y-axis) was represented in relation to their abundance values (x-axis). We identified the posterior mean of abundance (dotted and dashed black lines) and the 95% confidence intervals (dashed grey lines).

II. RESULTS & DISCUSSION

We estimated deer abundance on East Limestone to range between 30 and 44 deer with an average of 36 deer (i.e. 88 deer/km² with a 95% confidence interval between 73 and 107 deer/km²). This result may be surprising given that deer abundance was estimated to 16 deer in May 1996 on East Limestone during a survey that counted all individuals detected by a line of 10 observers walking across the island (Daufresne & Martin 1997). However, this survey did not account for fawn number (estimated at 15% of deer population) and direct observations and capture sessions conducted in 2011 and 2012 enabled to identify a minimum number of 29 deer (including fawns).

On Kunga, for the unique session with a converging model (see Figure SM.I.1.2 B) we estimated the deer abundance to be on average equivalent to 91 deer with a 95% confidence interval between 23 and 290 deer, say a density of 43 deer/km² with a 95% confidence interval of 11 and 136 deer/km². This broad confidence interval results from a long distribution tail towards large values and echoes Chandler & Royle's study which suggested that estimate accuracy decreases when the proportion of marked individuals in the population decreases (i.e. here only 3 marked deer detected on the pictures).

CONCLUSION

In a nutshell, deer abundance could be estimated on both islands. Confidence intervals highlighted important levels of variability in these population estimates, particularly for Kunga. Therefore we explored the effect of such variability on the energy model outputs (see section SM.I.2). Despite uncertainties, the confidence interval of deer abundance obtained on Kunga encompassed the one obtained for East Limestone, in agreement with previous plant survey data suggesting that both islands had been subject to comparable browsing pressure (Chollet 2012). Moreover, based on previous knowledge on deer abundance on East Limestone, we suspect that abundance estimates slightly overestimated the actual deer abundance on these islands. Such an overestimation would lead to overestimating the energy requirements of deer populations and hence ensure conservative results in the associated study.

SM.I.2. PARAMETER VARIABILITY AND SIMULATIONS

I. MATERIAL & METHODS

To control for the variability in the three main parameters estimated in the field (i.e. available dry biomass, deer population abundance and deer body mass) we conducted 5,000 simulations with randomly selected values for these parameters as follow: i) For the resource model, for each species in each resource we chose at random the annual dry biomass value within a normal distribution calibrated with the mean and standard deviation equaled to those observed in the field. Negative biomasses were counted as null. We computed for each set of simulated dry biomasses the energy available for each resource and the overall energy available on each island and each season; ii) For the deer model, for each simulation we chose at random the deer population abundance and deer body mass within normal distributions calibrated with the means and standard deviations equaled to those estimated by the CMR model for deer abundance and equaled to those measured in the field, respectively. For body mass, we used a single standard deviation estimate per age class on each island, estimated as the maximum value of standard deviations assessed for the given age class between both sexes and seasons. This ensured conservative results. Abundance and body mass estimates were checked to be equal or superior to the 2.5% quantile of the deer abundance distribution of the given island, and to the minimum body mass measured in the field for the given sex and age class, respectively (Table SM.I.2). When the estimates fell below these thresholds they were counted equal to these thresholds.

For both models (i.e. resource and deer models) we calculated for each season (i.e. summer and winter) the average and the 95% confidence interval of the energy available to and required without or with reproduction by the deer populations. To compare these levels of energy we proceeded as in the main text: we computed for each season the proportion of deer maintenance energy requirements (including thermoregulation costs) met by each resource as well as the total energy available for each season and for each habitat scenario (i.e. in the absence or presence of windfall). To compare the energy requirements including reproductive costs with the energy resources available, we assessed the proportion of energy required by the

deer model including reproductive costs as a function of the energy required as estimated by the model including maintenance costs only and compared it with the proportions calculated for the energy resources.

Table SM.I.2: Parameter ranges used to compute 5,000 simulations of deer energy requirements

		East Limestone		Kunga	
Deer Abundance (mean \pm standard deviation, minimum value)					
		36 +/- 4, min =30		168 +/-123, min = 42	
Body Mass (mean \pm standard deviation, minimum value in kg)					
Sex-age class	Summer	Winter	Summer	Winter	
female adult	34 \pm 12, min=31	33 \pm 12, min=28	32 \pm 10, min=24	29 \pm 10, min=27	
male adult	43 \pm 12, min=33	36 \pm 12, min=32	42 \pm 10, min=30	38 \pm 10, min=35	
female subadult	28 \pm 6, min=21	23 \pm 6, min=21	24 \pm 5, min=18	21 \pm 5, min=18	
male subadult	24 \pm 6, min=20	24 \pm 6, min=20	26 \pm 5, min=22	25 \pm 5, min=22	
fawn		18 \pm 3, min=15		14 \pm 3, min=12	

In the following analysis, minimum, maximum and average levels of energy refer respectively to the 2.5% quantile, 97.5% quantile and average values of the energy available to or required by the deer populations. To test the robustness of our models, we proceeded in three steps: i) we focused on the energy balance between the average levels of energy available and required; ii) we focused on the energy balance between the minimum levels of energy available and the average levels of energy required by deer populations; iii) we focused on the energy balance between the average levels of energy available and the maximum levels of energy required. This approach aimed to focus on simulation combinations that would make sense biologically. In particular, it excluded extreme approaches such as the least (i.e. maximum energy available vs. minimum energy required) and the most conservative approaches (i.e. minimum energy available vs. maximum energy required) that informed on the limits of our models but had little biological relevance to identify overall energy patterns.

As we observed similar patterns for both scenarios (i.e. in the absence or presence of windfall, Figure SM.I.2.1, SM.I.2.2) the present analysis focused on the scenario in the absence of windfall and numerical values cited below referred to this scenario. However results described here were also relevant for the scenario in the presence of windfall as well and the main points discussed concerned both scenarios.

II. RESULTS & DISCUSSION

Energy Balance: average levels of energy available vs. average levels of energy required

In summer, the average levels of energy available to deer covered > 230% of the average level of energy required by the reproductive deer populations on both islands (see Figure SM.I.2.1 A,C). In winter, however the energy available covered only 44 and 87% of the energy required by East Limestone and Kunga deer populations, respectively (see Figure SM.I.2.1 B,D). This reflected the overall pattern described in the main text.

Energy Balance: minimum levels of energy available vs. average levels of energy required

During the summer, the minimum levels of energy available to deer covered only 52 and 104 % of the maintenance requirements of the East Limestone and Kunga deer populations and only 43 and 90 % of the energy requirements of the reproductive deer populations on East Limestone and Kunga, respectively (see Figure SM.I.2.1 A,C). In winter, the energy available covered only 6 and 11 % of the energy required by East Limestone and Kunga deer populations, respectively (see Figure SM.I.2.1 B,D).

In this case, energy deficits were present for both seasons (i.e. summer and winter). Such pattern (i.e. the energy available in summer did not meet the average energy requirements for the reproductive deer populations) concerned 16 and 3% of the simulations conducted on East Limestone and Kunga, respectively. Thus, at a threshold of 16%, the global pattern described in the main text (i.e. energy deficit in winter and energy excess in summer) was supported by the simulations.

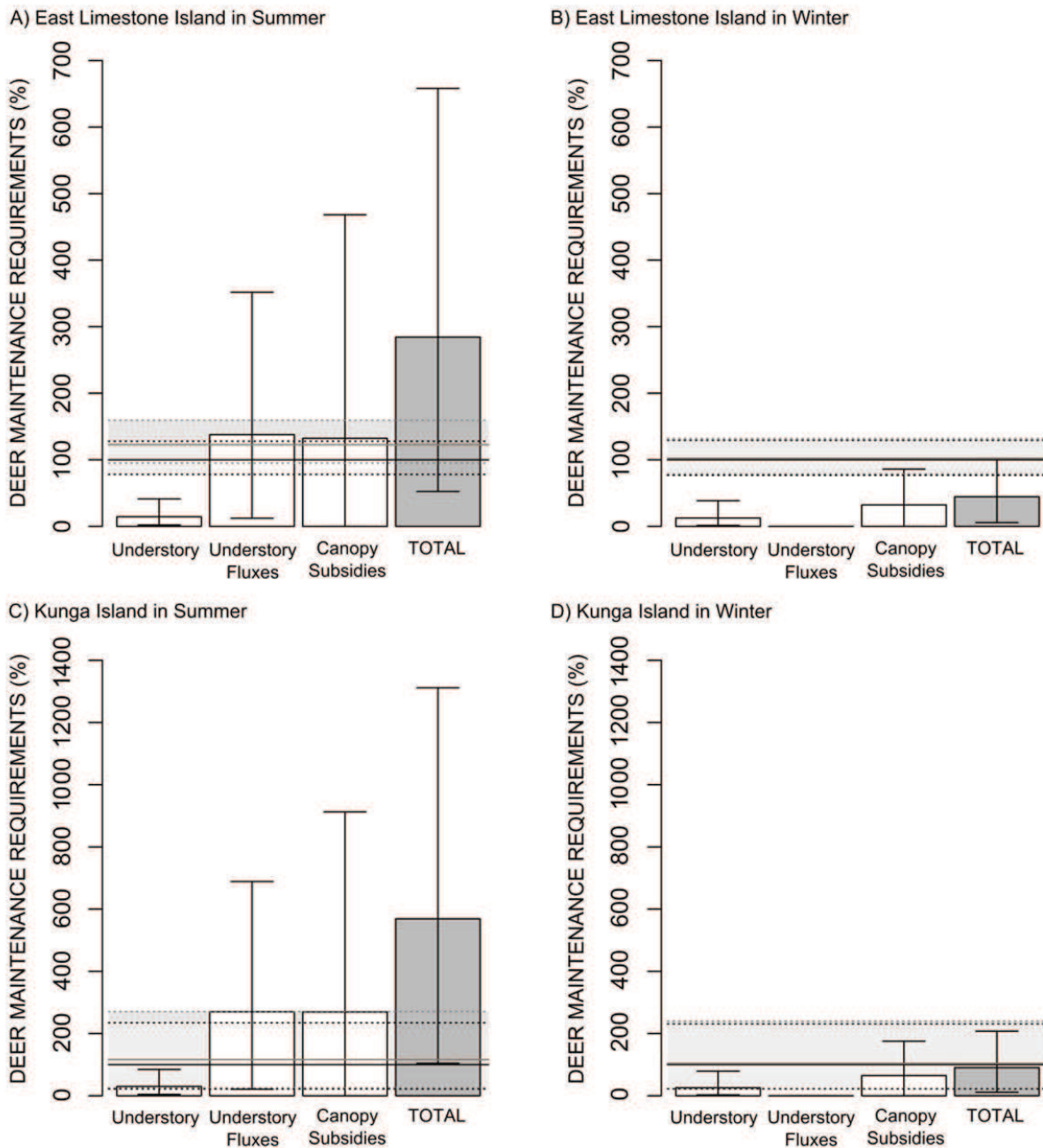


Figure SM.I.2.1: Energy balances on East Limestone (A ,B) and Kunga (C, D) under the scenario in the absence of windfall areas. Percentages (mean +/- 95% confidence interval) of energy resources available from the understory, the understory fluxes and the canopy subsidies in relation to the deer maintenance requirements are presented. The black lines mark 100% of the average maintenance energy requirements of the local deer populations. The grey lines mark the average energy requirements with reproductive costs. 95% confidence interval of maintenance energy requirements (dark grey zones) and of energy requirement with reproduction costs (light grey zones) are delimited by dark and grey dashed lines respectively for energy requirements without and with reproduction costs.

Energy Balance: average levels of energy available vs. maximum levels of energy required

In summer, the average energy available covered > 175% of the maximum energy requirements of the reproductive deer populations on both islands (see Figure SM.1.2.1 A,C). In winter, the energy available covered only 34 and 38 % of the energy required by the reproductive deer populations on East Limestone and Kunga, respectively (see Figure SM.1.2.1 B,D). In this case, the global overall pattern described in the main text was confirmed.

CONCLUSION

The main pattern observed over these simulations was an overall energy deficit in winter ranging from 30 to 60% of the energy requirements of reproductive populations and an overall large amount of energy available in summer exceeding the energy requirements of deer populations by almost 200%. This pattern was observed for the majority of the simulations: in >70% and >90% of simulations conducted on East Limestone and Kunga, respectively, the energy available covered >146% of the energy requirements of the reproductive deer populations in summer (with 146% the energy levels estimated with the average values measured in the field). This pattern was especially observed for the complete 95% confidence interval on deer abundance, considered as a major source of variability in the model including very high deer density (i.e. 105 deer/km²). Therefore we were confident on the overall robustness of the pattern presented in the main text.

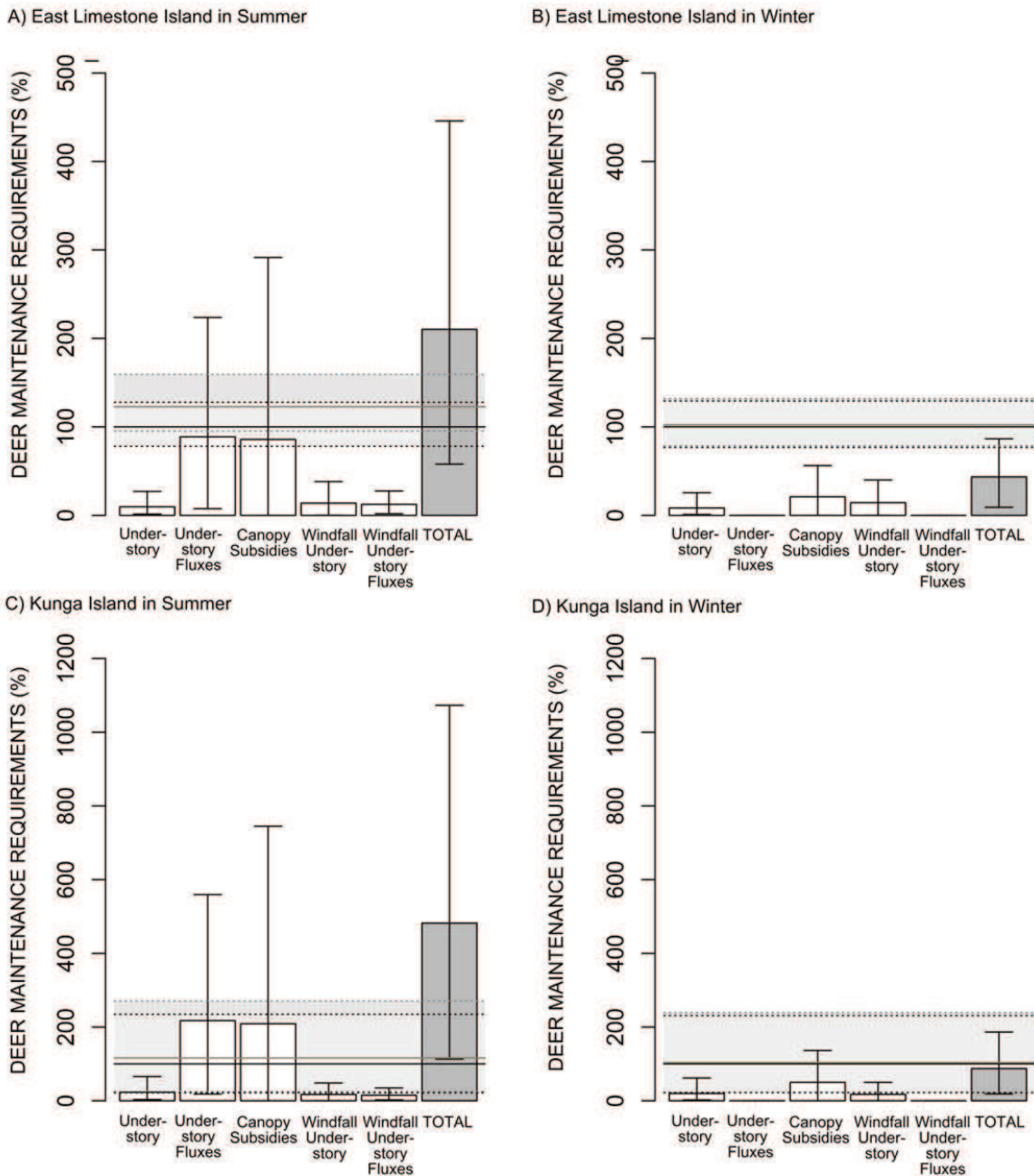


Figure SM.I.2.2: Energy balances on East Limestone (A ,B) and Kunga (C, D) under the scenario in the presence of windfall areas. Percentages (mean +/- 95% confidence interval) of energy resources from the understory, the understory fluxes and from the canopy subsidies in intact forest areas and from the understory and from the understory fluxes in windfall areas in relation to the deer maintenance requirements are presented. The black lines mark 100% of the average maintenance energy requirements of the local deer populations. The grey lines mark the average energy requirements with reproductive costs. 95% confidence interval of maintenance energy requirements (dark grey zones) and of energy requirement with reproduction costs (light grey zones) are delimited by dark and grey dashed lines respectively for energy requirements without and with reproduction costs.

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COMPLEMENTARY ANALYSIS I

DEER DENSITY AND ENERGY BALANCE ON REEF

For comparison and to better understand the relationship between deer and their environment, we conducted the same approach on the deer population of Reef. We first assessed deer density from a capture-mark-recapture (CMR) analysis using camera trap data. We then assessed deer balance energy by comparing the energy available to and required by the local deer population. Methods used were strictly similar to those presented for East Limestone and Kunga. Here we only described specificities of the experimental design and parameters used to estimate the density and energy balance of deer population on Reef.

I. DEER DENSITY ESTIMATED BY CMR METHOD

I.A. EXPERIMENTAL DESIGN

To assess deer density we surveyed 13 sites during seven consecutive days (i.e. seven capture occasions) with a surveyed area estimated to cover 98% of the island area (i.e. 243 ha). Only the extreme South and East points were not covered, thus we considered that the density estimated by this camera trap survey was representative of the average density on the whole island. During the camera-trap survey we recorded 72 deer visits (captures) among which seven were made by marked deer. At the time of the survey only four deer were marked and three of them were detected on the pictures.

I.B. MODEL PARAMETERS

To estimate deer density, we used Chandler & Royle's model (2013) using the following prior values (Table CA.I.1): with M being the maximum abundance value accepted in the model, σ a scale parameter determining the rate of decay in encounter probability, λ_0 the encounter rate for a null distance between an activity center and a camera site, ϕ the parameter of data augmentation and S the activity center matrix (SM.I.1 and Chandler & Royle 2013).

Table CA.I.1: Prior values used to estimate deer abundance on Reef

M	σ	λ_0	ϕ	Tune for σ	Tune for λ_0	Tune for S
300	[80 – 300]	[0.05 – 1]	[0 – 1]	30	0.1	300

I.C. RESULTS & DISCUSSION

We estimated deer abundance on Reef to be 42 individuals [95% CI: 24; 70] in the 243-ha surveyed area (i.e. 17 deer/km² with a 95% confidence interval between 10 and 29 deer/km²; Figure CA.I.1). This result is in agreement with a previous estimate of deer density on Reef based on historical data and approximate life-history data. Indeed, in a simple demographic model using a growth rate of 1.2 and including deer harvest rate, Chollet et al. (in prep) estimated that the current deer density should be c. 10-15 deer/km². Chollet’s estimate fell thus within the confidence interval estimated by the CMR analysis [95% CI: 10; 29 deer/km²], although at the lower range of the interval. Whether true deer density on Reef is closer to 10 or to 20 deer/km² cannot be assessed. However, because the CMR method tended to overestimate deer density on East Limestone (SM.I.1), it is possible that the CMR estimate of deer density on Reef would also be slightly overestimated. If true, this should not bias the energy balance analysis, as it would overestimate deer energy requirements, providing thus conservative results. In the present study, we used 17 deer/km² as density estimate on Reef.

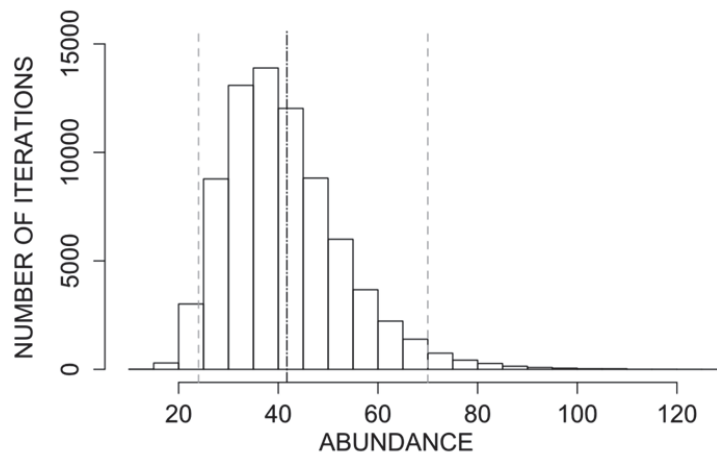


Figure CA.I.1: Distribution of deer abundance estimated on Reef. The number of iterations considered in the analysis (i.e. the last 25000 iterations among the 30000 simulated) (y-axis) was represented in relation to their estimates of deer abundance (x-axis). We identified the posterior mean of abundance (dotted and dashed black lines) and the 95% confidence intervals (dashed grey lines).

In comparison with average deer densities estimated on East Limestone (c. 88 deer/km², [95% CI: 73 ; 107]) and Kunga (c.43 deer/km², [95% CI: 11 ; 136]), average deer density on Reef was 2.5 to 5 times lower. However, the confidence interval estimated for deer density on Reef fell within the wide confidence interval estimated for deer density on Kunga. The fact that Kunga's confidence interval included both East Limestone and Reef's confidence intervals may prevent from finer comparisons between islands. However, previous plant surveys reported that Kunga, like East Limestone, presented depleted forest understory exposed to heavier deer browsing pressure, whereas Reef presented a partially recovered understory exposed to limited browsing pressure (Chollet et al. in prep; Le Saout 2009; Martin et al. 2010). In addition, estimates of deer body mass on Kunga were similar to these on East Limestone and seemed lower than these assessed on Reef, although the comparison is limited given the few measures available on the latest (Table I.2, Table CA.I.2). Therefore, we considered that despite the large confidence interval of the population density estimated for Kunga, true deer density on Kunga is more likely to be close to the one observed and estimated on East Limestone. Deer density on Reef is thus likely to be at least 2.5 times lower than the one on East Limestone and Kunga.

II. DEER ENERGY BALANCE ON REEF

To assess deer energy balance on Reef, we proceeded as described in Chapter I for East Limestone and Kunga. First we estimated the energy available to the deer population via the resource model. Secondly, we estimated the energy required by the deer population via the deer model. Thirdly, we compared both estimates. Fourthly, we controlled the robustness of our results in running 5000 simulations with randomly selected values for plant biomass, deer density and deer body mass. A detailed presentation of the method used is provided in Chapter I and supplementary materials (SM.I.2). Here we provided only the specificities of the experimental design to assess plant biomass and deer demographic parameters.

II.A. RESOURCE MODEL: EXPERIMENTAL DESIGN TO ESTIMATE PLANT BIOMASS

To estimate (i) the annual biomass provided by the “understory” resource, we monitored 10 transects in the intact forest areas and 12 transects in the windfall areas. To estimate (ii) the biomass provided by the “understory fluxes”, we monitored ten exclosures in the intact forest and four in the windfall areas. In May 2011 we removed all green biomass from a 1-m² field-layer in each exclosure. A year later, in May 2012, we collected the biomass that had grown over the year in these exclosures. An exclosure in the windfall areas enabled the growth of a 1.3-m height red elderberry shrub (*Sambucus racemosa*). This exceptional growth generated an average biomass flux 10 times higher than the one recorded in the intact forest on Reef. It was also 60 times higher than the average biomass flux estimated in windfall areas on East Limestone and Kunga. Therefore, we considered this exclosure to be an outlier which would have strong leverage in our analysis due to our small sample size and excluded it from the analysis. To estimate (iii) the biomass provided by the “canopy subsidies”, we monitored 10 litterfall traps set in the intact forest. We collected the monthly biomass fallen in each trap in June and July 2011. As for East Limestone and Kunga, we assessed the energy available to deer under two habitat scenarios: the first one not accounting for windfall areas and the second one accounting for windfall areas. Under the scenario accounting for windfall areas, windfall areas were estimated to cover 15% of Reef area.

II.B. DEER MODEL: ASSESSMENT OF DEER DEMOGRAPHIC PARAMETERS

As for East Limestone and Kunga we estimated the following demographic parameters: (i) population abundance; (ii) sex ratio; (iii) age ratio; (iv) body mass of each sex and age class; and (v) reproductive investment of each sex and age class.

(i) We used the deer density value estimated with the CMR method (i.e. 17 deer/km², see above) and considered that 43 deer were present on the whole island (249 ha).

(ii,iii) As for East Limestone and Kunga, we estimated both sex and age ratios via the camera-trap survey used for the CMR method. Over the 72 visits recorded, we estimated female sex ratio to be 0.58. Age ratio estimates are detailed in Table CA.I.2.

(iv) We estimated the average body mass of each sex and age class for each season via deer captures during which we sexed, aged, weighed and marked individuals with ear tags. On Reef, capture sessions occurred in late winter (March) 2012 and early fall (August-October) 2011 and 2012. Overall, we captured seven individuals (3 females, 4 males). As for East Limestone and Kunga, we used the data from early fall and late winter captures to estimate the average summer and winter body mass of each sex and age class, respectively. However, given the limited number of captures (a total of 6 individuals were captured during the fall sessions and of 3 individuals during the winter session), we used broader estimates for body mass based on inflated values of measured body mass (Table CA.I.2). This was thought to ensure conservative results. We considered that body mass was constant over a season.

(v) Data on reproductive investment were limited for Reef. Only an adult female was captured and it had a single fawn, and only a subadult female was captured and had no fawns. On camera trap, only two visits of a female with a fawn were observed. Although deer reproduction strategy may be expected to change accordingly to resource availability and deer density (Bonenfant et al. 2009), we considered that Reef deer would follow the same reproduction regime as East Limestone and Kunga deer in the model : i.e. subadult females did not invest in reproduction and only adult females reproduced and had a single fawn. Similarly to East Limestone and Kunga deer, we considered that both subadult and adult males invested in

reproduction. This may underestimate deer energy requirements, however, based on the data available, we could not estimate if and how deer reproduction strategy would differ between Reef and East Limestone and Kunga.

Table CA.I.2: Deer age-ratio and body mass on Reef. We reported for each season (winter and summer) and age class (adult, subadult and fawn) the age ratio obtained from camera-trap data as well as the average body mass values estimated for each season, sex and age class. When available we provided the mean value \pm standard deviation and the number of individuals (n) on which body mass estimates were assessed. Due to very limited sample size, we used inflated body mass estimates in the deer model.

Parameters	Season	Adult	Subadult	Fawn
Age Ratio	Winter	0.51	0.41	0.08
	Summer	0.51	0.49	
Body mass measured in the field (kg)	Winter	Female: NA Male: 53 (n=1)	Female: NA Male: 30 (n=1)	17 (n=1)
	Summer	Female: 36 (n=1) Male: 54 (n=1)	Female: 28 (n=1) Male: 34 \pm 7 (n=1)	
Inflated body mass estimate used in the deer model (kg)	Winter	Female: 40 Male: 55	Female: 35 Male: 35	20
	Summer	Female: 40 Male: 55	Female: 35 Male: 35	

II.C. DEER ENERGY BALANCE

Deer energy balance was largely positive during summer and winter under both scenarios (without or with windfall areas). Under both scenario, the energy available to deer met > 1600% of the energy required by the reproductive deer population in summer and > 700% of the energy required by the reproductive deer population in winter (Figure CA.I.2). Remarkably, the energy provided by the understory met > 700% of the energy requirements of the reproductive deer populations and provided > 90% of the energy available to deer in winter. Deer energy balance appeared thus to remain positive even in the winter thanks to the large amount of energy provided by the understory.

To assess the robustness of this result we re-run simulations with different parameters for plant biomass, deer density and deer body mass.

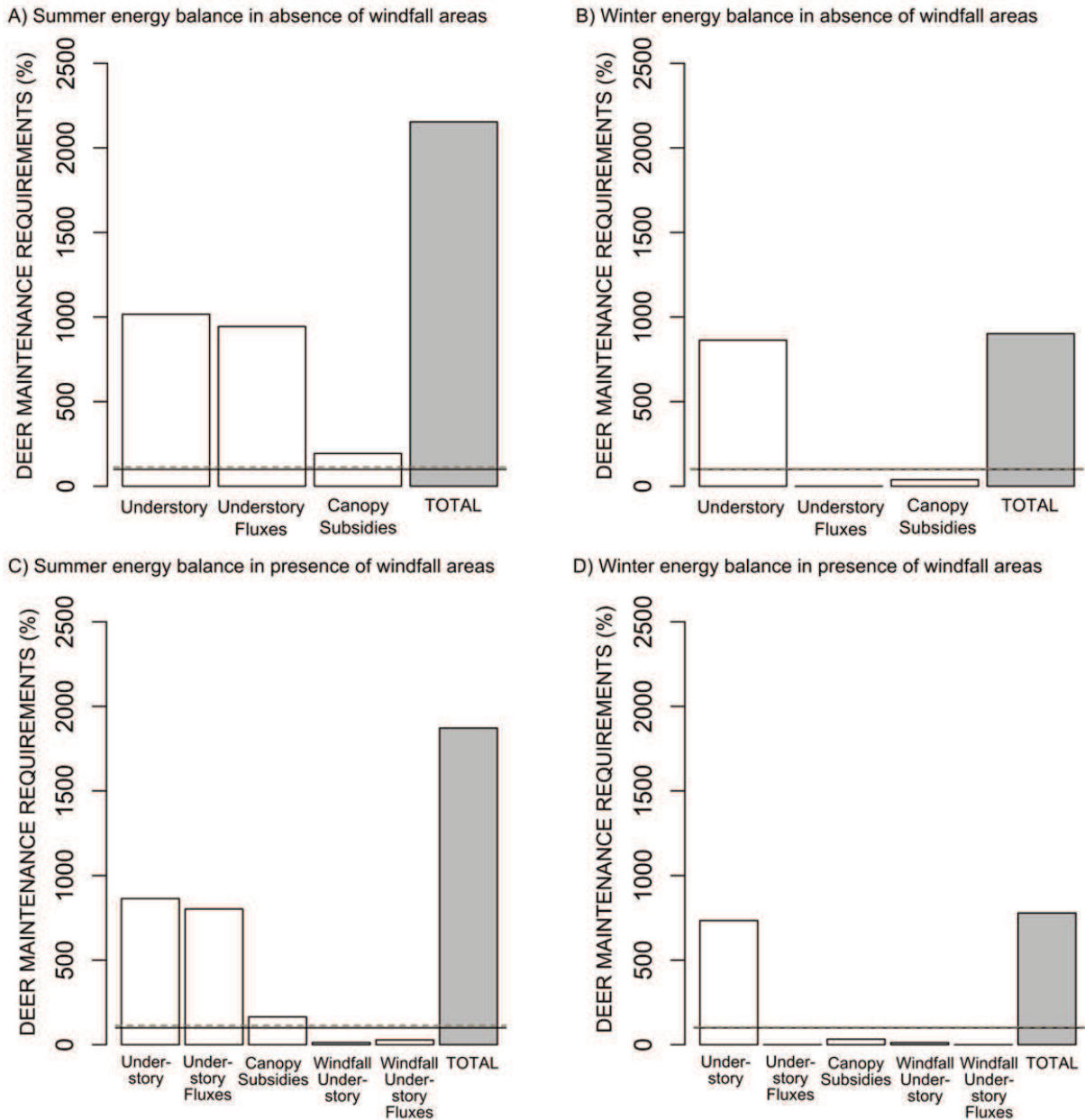


Figure CA.1.2: Estimated energy balances on Reef in summer (A,C) and winter (B,D) under the scenario not accounting for windfall areas (A,B) or accounting for windfall areas (C,D). Open bars give the percentage of the deer maintenance energy requirements (i.e. energy needed to maintain the studied deer populations without accounting for reproductive costs) that are covered by the energy available from each type of resource (i.e. understory, understory fluxes and canopy subsidies in forest areas and understory and understory fluxes in windfall areas). The grey bars give the sum of the white bar values (i.e. the total percentage of the maintenance energy requirements of the deer population covered by all resources available). The solid lines refer to the level of energy needed to maintain the deer populations without accounting for reproductive costs (100%). The dashed lines refer to the energy requirements of the deer populations when accounting for reproductive costs (i.e. 114% in summer and 103% in winter). Due to the large amount of energy available to deer, solid and dashed lines, which mark the level of energy required for maintenance only or for maintenance and reproduction, respectively, are mostly overlapping.

II.D. SIMULATED ENERGY BALANCE AND MODEL ROBUSTNESS

II.D.1. PARAMETER SETS

As for East Limestone and Kunga we explored the sensitivity of our results to the three main parameters estimated in the field (i.e. plant biomass, deer abundance and deer body mass). As detailed in supplementary materials SM.I.2, values for these parameters were randomly selected within normal distributions with the mean and standard deviation equal to those observed in the field for plant biomass and to those estimated by the CMR method for the deer abundance (i.e. 43 ± 12 deer). For deer body mass, we used standard deviation values of 10 kg for both adults and subadults and a value of 5 kg for fawns. We used the 2.5% quantile of the deer abundance distribution as minimum abundance (i.e. 24 deer) and fixed the minimum body mass values to 40 kg for adult males, 30 kg for adult females, 25 kg for subadults and 15kg for fawns. Standard deviations and minimum values for body mass were arbitrarily fixed considering that Reef deer should have body mass values higher or at least within the upper range of body masses recorded for East Limestone and Kunga deer.

II.D.2. RESULTS & DISCUSSION

Overall the pattern observed with the values measured in the field remained: deer energy balance was positive in summer for all simulations under the scenario without windfall and for > 99.9% of simulations under the scenario with windfall areas. Deer energy balance was also positive in winter for $\geq 97\%$ of simulations under both scenarios. In particular, about 70% of simulations under both scenarios presented summer and winter energy balances with respective levels of energy available to deer $\geq 1600\%$ and $\geq 700\%$ of the levels of energy required by the reproductive deer population (values obtained with the parameter estimates measured in the field).

In addition, the understory biomass remained the principal source of energy and particularly in winter when it provided > 70% of the energy available to deer in about 90% of the simulations. Remarkably, the understory biomass provided less than 50% of the energy available to deer in only 5% of the simulations. Finally, when comparing the average level of energy available to

deer (i.e. “average resource model”, see SM.I.2) with the upper range of the levels of energy required by deer (“maximum deer model”: see SM.I.2), the understory met > 880% of the energy requirements of the reproductive population in summer and winter. This highlighted the important contribution of understory to deer energy balance in particular in winter when other food resources are limited.

CONCLUSION

To conclude, as for East Limestone and Kunga, the pattern assessed for the deer energy balance on Reef was robust to possible errors in field measurements of plant biomass, deer abundance and deer body mass. As expected, Reef deer have access to a large amount of resources and in particular the partially recovered forest understory was a major contributor to the energy available to the local deer population. Although changes in reproduction strategy may increase the level of energy required by the deer population in summer, the large excess of energy available to deer during the summer and winter is likely to cover these needs. Thus, we considered that the qualitative pattern observed on Reef is robust. Deer energy balance is likely to remain positive all over the year, and deer are unlikely to suffer from strong winter starvation contrary to East Limestone and Kunga deer.

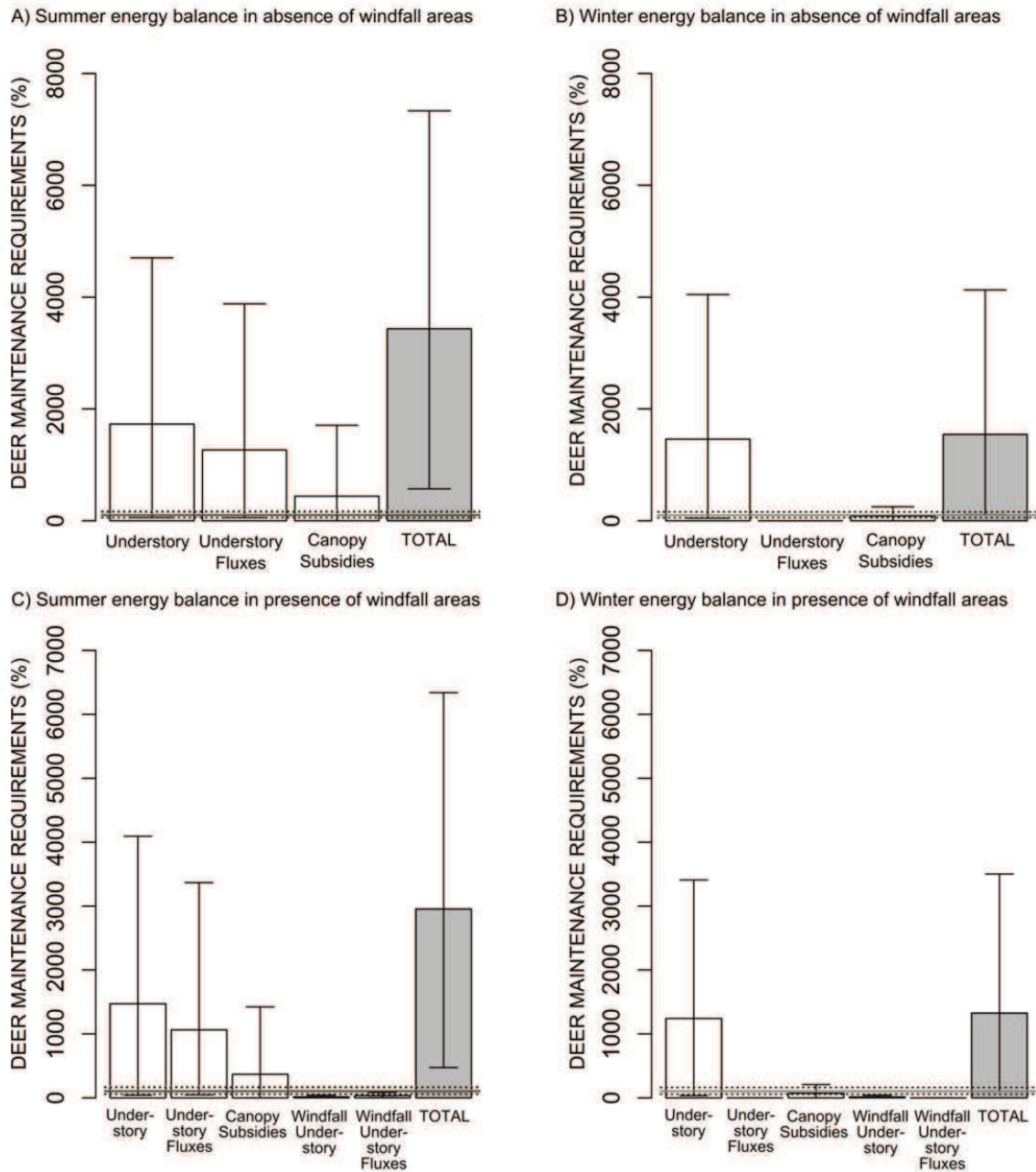


Figure CA.1.3: Simulated energy balances on Reef island in summer (A,C) and winter (B,D) under the scenario not accounting for windfall areas (A,B) and under the scenario accounting for windfall areas (C,D). Open bars give the percentage (mean +/- 95% confidence interval) of the deer maintenance energy requirements (i.e. energy needed to maintain the studied deer populations without accounting for reproductive costs) that are covered by the energy available from each type of resource (i.e. understory, understory fluxes and canopy subsidies in forest areas and understory and understory fluxes in windfall areas). The grey bars give the sum of the white bar values (i.e. the total percentage of the maintenance energy requirements of the deer population covered by all resources available). The black lines mark 100% of the average maintenance energy requirements of the local deer populations. The grey lines mark the average energy requirements with reproductive costs. 95% confidence interval of maintenance energy requirements (dark grey zones) and of energy requirement with reproduction costs (light grey zones) are delimited by dark and grey dashed lines respectively.

SUMMARY

We estimated that deer density on Reef was likely to be at least 2.5 times lower than the density on East Limestone and Kunga. Contrary to East Limestone and Kunga where deer are likely to suffer from food shortage in winter, deer energy balance was positive over the year, including winter time, thanks to its rich and abundant understory. Indeed, Reef understory was a major contributor to the energy available to deer and generally exceeded deer energy requirements. This confirmed that Reef on the one hand and East Limestone and Kunga on the other hand present two contrasted environments for deer: the less abundant deer population on Reef has access to a large amount of resources, likely to exceed deer energy requirements at any time of the year, whereas the denser deer populations on East Limestone and Kunga maintain reproductive populations, but are likely to experience food shortage in winter.

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CHAPTER II:

**LOW FOOD ABUNDANCE OR PREDATION RISK: WHAT IS MOST
STRESSFUL FOR INSULAR BLACK-TAILED DEER?**

CHAPTER II: LOW FOOD ABUNDANCE OR PREDATION RISK: WHAT IS MOST STRESSFUL FOR INSULAR BLACK-TAILED DEER?

“We assayed deer FGM [Fecal Glucocorticoid Metabolites] in 205 fecal samples [...], we estimated seaweed consumption using micro-histological analyses and investigated its relationship with FGM levels”

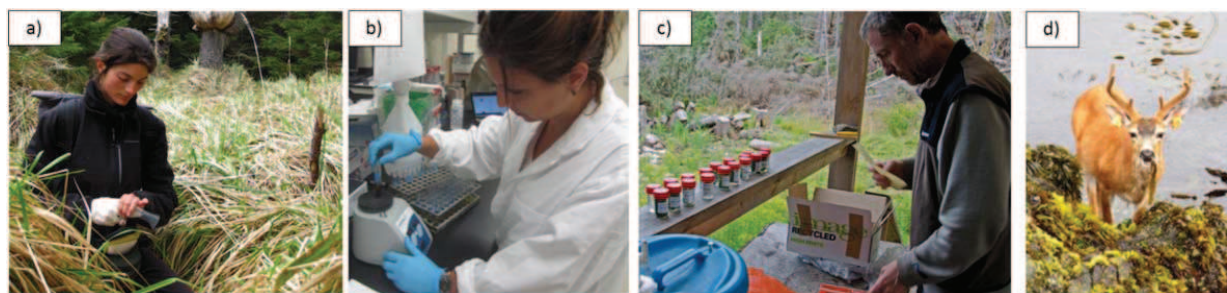


Figure B: Study of the levels of fecal glucocorticoid metabolites (FGM) in contrasted situations of food abundance and predation risk and of the possible effects of seaweed consumption. (a) Fresh fecal sample were collected monthly (T. Verchère). (b) Hormone assay is conducted on fecal samples. (c) We created a reference database of local plants to conduct micro-histological analyses on the fecal sample (J.L. Martin); (d) Deer feeding on seaweeds on Kunga (S. Padié).

in preparation for Wildlife Society Bulletin

CHAPTER II: LOW FOOD ABUNDANCE OR PREDATION RISK: WHAT IS MOST STRESSFUL FOR INSULAR BLACK-TAILED DEER?

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KEYWORDS: cortisol, HPA axis response, cervids, predator-free islands, chronic stress, hunting, food shortage

ABSTRACT

During their lifetime, animals face various stressors and mount a physiological stress response to cope with them. Although animal physiological responses to a wide range of stressors have been studied, fewer studies have compared stressors and their relative impacts on animal physiology. Here we compared two different stressors: low food abundance and predation risk in free-ranging Sitka black-tailed deer (*Odocoileus hemionus sitkensis*). We compared over a year monthly levels of fecal glucocorticoid metabolites (FGM), an indicator of animal physiological stress, between three insular deer populations : two were not predator-free but exposed to food depletion and starvation risk (in winter) and the third had access to abundant food but was exposed to hunting and related human activities. We expected FGM levels to be higher in winter when food is rarer in the former situation and to be higher when humans are present in the latter one. We ascertained seasonal and inter-island differences in food quality by measuring fecal nitrogen content. Deer populations presented similar average FGM levels (c. 20 ng/g) and similar seasonal variations independently from food abundance and predation risk. FGM levels increased in late spring-summer, associated with increasing energy demand for reproduction (antler growth, end of gestation and lactation), but did not increase in response to lower food abundance in winter or to more intense human activities. We interpret this absence of stress response as behavioral and/or physiological adjustments, limiting deer exposure to either stressor. Despite prolonged exposure to moderate stressors, deer seem to be able to cope with the situations without mounting chronic stress responses.

INTRODUCTION

During their lifetime, animals face various stressors, defined as events or factors that perturb their homeostasis (Reeder & Kramer 2005). Stressors may be abiotic (e.g. temperature, pollutants) or biotic (e.g. predation, competition, social interactions, diseases) (review in Wingfield 2003) and may last for minutes or hours (e.g. Wingfield et al. 1995; Bateson & Bradshaw 1997) to days, weeks or years (e.g. Boonstra et al. 1998; Romero & Wikelski 2001).

To reestablish their internal equilibrium animals mount a stress response, a physiological cascade mediated by various hormones (review in Sapolsky et al. 2000; McEwen & Wingfield 2003; Romero 2004; Reeder & Kramer 2005). Among others, glucocorticoids, a family of steroid hormones, orchestrate the mobilization and re-allocation of energy that is required when the animal engages in behaviors that are fundamental for its survival (e.g. aggression, social challenges, escape: Wingfield 2003). Increasing glucocorticoid levels are thus generally an adaptive response to an acute stressor. However, prolonged exposure to high levels of glucocorticoids has deleterious effects, for instance negative impacts on growth, reproduction and long-term survival (e.g. immunodepression) (review in Sapolsky et al. 2000; Romero 2004; Reeder & Kramer 2005). Clarifying how animals modulate their glucocorticoid-based stress response is thus an important challenge to understand animal response to a changing environment (McEwen & Wingfield 2003; Romero & Butler 2007; Busch & Hayward 2009; Wingfield 2013).

The stress response can be assessed indirectly in feces and urine as glucocorticoid metabolites are excreted in both feces and urine (Taylor 1971; Palme et al. 2005). Fecal glucocorticoid metabolites (FGM) are convenient stress indicators because their estimation does not require invasive sampling methods and they integrate the physiological energy demand over daily periods (review in Millspaugh & Washburn 2004; Keay et al. 2006; Sheriff et al. 2011b). For a variety of taxa FGM levels have been found to increase during the reproductive season in presence of food shortage and during harsher climatic conditions (e.g. Huber et al. 2003; von der Ohe et al. 2004; Dalmau et al. 2007; Herring et al. 2011) as well as under predation risk (e.g. Monclús et al. 2009; Sheriff et al. 2011a) or when animals are exposed to human activities (e.g. Creel et al. 2002; Thiel et al. 2011). However, this is not always the case (e.g. Taillon & Côté

2008; Creel et al. 2009) and behavioral and/or physiological adjustments may co-occur producing diverse stress responses in animals (Wingfield et al. 1995; Wingfield 2003; Wingfield & Sapolsky 2003; Busch & Hayward 2009).

Animal physiological stress responses have been studied for a wide range of stressors, but comparative studies of the effect of different stressors on animal stress response have been rarely conducted in the context of the same study (Angelier & Wingfield 2013). This issue is particularly complex to study in the wild as many factors can co-vary over time or space. Using a unique cross-factorial semi-experimental approach on song sparrows (*Melospiza melodia*), Clinchy et al. (2004) showed that the baseline levels of glucocorticoids in birds exposed to either starvation or predation risk were similar and at an intermediate level between those assessed in birds exposed to none or both stressors. These results were obtained on birds during the breeding season, and further studies are thus required to conclude on the relative importance of both stressors (food abundance and predation risk) in different systems. To the best of our knowledge, except for Clinchy et al. (2004)'s experiment no other studies investigated simultaneously the response to two or more stressors. Many studies have investigated the effect of one stressor on glucocorticoid levels (e.g. diet quality: Kitaysky & Piatt 1999; social environment: Sands & Creel 2004; predation risk: Rodl et al. 2007; Newman et al. 2013), while other studies have used seasonal changes in risk to assess the relative impacts of various stressors (e.g. diet quality, human disturbance, reproduction stage, climatic conditions: Millspaugh et al. 2001; Huber et al. 2003; von der Ohe et al. 2004). However, disentangling the various possible causal effects in stress response is difficult, particularly in the wild when factors are likely to co-vary. Thus, further studies using contrasted treatments, either experiments or field comparisons, are warranted.

Here we examined the relative importance of low food abundance and predation risk as stressors (indexed by FGM levels) in three neighboring insular populations of black-tailed deer living under contrasted situations of food abundance and predation risk in the Haida Gwaii archipelago (B.C., Canada). On two islands deer have been isolated from natural predation and from hunting for over 60 years. There, deer live at high density in forests with a severely depleted understory. They are likely to face strong constraints on foraging and resource

acquisition, especially in winter. On the third island deer were nearly extirpated in 1997 and have been exposed to chronic hunting since then. There, deer live under predation risk but benefit from a rich forest understory which has regenerated. Glucocorticoid levels are expected to increase in presence of food shortages (e.g. Saltz & White 1991a, 1991b; Saltz et al. 1992) as well as under predation risk (e.g. Boonstra et al. 1998). However, to our knowledge little is known on the relative effects of these two stressors in mammal species. FGM levels may be higher, lower or similar between the safe/poor and the risky/rich islands, according to how low food abundance or predation risk affect FGM levels. We predicted that: (1) FGM levels will increase in winter when food is limited. This is particularly expected on the safe/poor islands, where deer are more likely to experience risk of winter starvation. Indeed, although local deer populations may be able to maintain a positive energy balance over a year, winter time (when food resources are low) and early spring time (when fat storage should be rebuilt and females are pregnant) are critical periods and deer on these safe/poor islands are expected to suffer an overall energy deficit during these periods (Chapter I); (2) FGM levels may increase when humans, a potential disturbance, are actually present on the islands. This is, especially expected on the risky/rich island where deer should perceive humans as predators and not only as disturbing agents. We ascertained seasonal and inter-island differences in food available and deer diet quality by measuring fecal nitrogen content. Because we observed black-tailed deer feeding on seaweed and because there had been suggestions that dietary seaweed might affect glucocorticoids release in the blood (Archer et al. 2007), we estimated seaweed consumption using micro-histological analyses and investigated its relationship with FGM levels.

I. MATERIAL AND METHODS

I.A. STUDY AREA

The study took place on the East coast of the Haida Gwaii archipelago (British Columbia, Canada), on three islands located within 15 km from each other in Laskeek Bay: East Limestone (41 ha, WGS84-52.91N 131.61W), Kunga (395 ha, WGS84-52.77N 131.57W) and Reef (249 ha: WGS84-52,87N 131.52W) islands. The climate is cool temperate, oceanic, and humid-perhumid with narrow temperature variations around the average annual value of 8°C (Pojar 2008). All

islands are uninhabited, and human presence is restricted to the presence of rare tourist visits in summer and occasional research activities (from March to July and from September to October during the study period).

Deer were introduced on Haida Gwaii c. 100 years ago and reached the study islands over 60 years ago (Vila et al. 2004). There, in the absence of predation (natural and human), deer built up high density populations (estimated to be >30 deer/km² in 1996 (Daufresne & Martin 1997)) that dramatically reduced forest understory cover by $>90\%$. (Martin et al. 2010). In order to limit and reverse deer negative impacts on their environment, a cull started on Reef in 1997. The population was reduced by $>70\%$ within the three years following the first hunt (Gaston et al. 2008; Chollet et al. in prep). Between 1998 and 2010 the understory below the browse line increased between 150 and 900% in cover according to the height class considered, and plant species richness quadrupled (Chollet 2012). The understory on Reef has thus partially recovered and offers a rich and dense food resource to the remaining deer population. No cull occurred on East Limestone or on Kunga where the understory is devoid of most plant species recorded in the traditional diet of black-tailed deer (McTaggart Cowan 1956; Pojar et al. 1980; Martin et al. 2010). The remaining plants are mostly <50 cm in height, low in palatability (e.g. Sitka spruce) and ground is barren or covered with moss (Martin et al. 2010). Despite this apparent lack of food, East Limestone and Kunga deer populations persist at high-density, with deer feeding on annual growth of perennial plants surviving via underground structures (e.g. rhizomes) as well as on litterfall subsidies (Chapter I) and seaweeds (Poilvé 2013).

Contrary to the predator-naïve deer on East Limestone and Kunga, deer on Reef have been hunted regularly since 1997. Although hunting efforts were limited between 2003 and 2005, several days to weeks of hunting have occurred yearly since 2006 and the last successful hunt took place in June 2010, 6 months prior to the beginning of the study. No hunting occurred during the study period but researchers were present with daily fieldwork activities taking place on Reef from May to July 2011 as well as in September and October 2011. Reef deer usually avoid humans or flee at their sight (pers. obs.) and thus seem to perceive humans as unsafe. We thus expected deer to experience increased stress during the months with human presence and considered that human presence were perceived as predation risk by deer. In addition, East

Limestone, like Reef, serves as base camp for research and human activities are generally more intense on East Limestone than on Kunga, especially, between May and early July when East Limestone hosts small crews of volunteers (3-6 people). Deer on East Limestone may thus be more exposed to human presence than deer on Kunga in May and June. However, deer on East Limestone are still expected to be less stressed by humans than deer on Reef where deer have been hunted by humans and should perceive humans as predators.

I.B. COLLECTION OF FECAL SAMPLES

On each study island, we collected 8 to 12 fresh fecal samples monthly from April 2011 to July 2011, as well as in late August- early September 2011, in October 2011, and in March 2012. For a given month, we sampled the three islands within a week, except in October 2011 when the last island was sampled two weeks after the first one. For each month, we collected all fecal samples on a given island within a day except on Reef in May and June 2011 when sample collection took place over two days. The collections were distributed across the islands and were spatially distributed in a way to minimize the risk of repeated sampling of the same individuals. Mean distances (mean \pm sd) between samples were estimated to be c. 200 ± 30 m on East Limestone and c. 700 ± 200 m on Kunga and Reef. We identified fresh feces from the presence of a fresh mucous membrane and collected 15 to 20 pellets per fecal samples. We placed each sample in an individually labeled airtight plastic bag and stored them frozen at c. -20°C . In the laboratory, fecal samples were dried for 7-9 days at 50°C and divided into three parts: one was ground at c. 5.0 ± 0.5 mm and kept frozen (-20°C) until FGM assay, one was ground at $125 \mu\text{m}$ and stored at room temperature until nitrogen (N) assay and the last part was not ground and kept at room temperature until micro-histological analyses.

I.C. FGM ANALYSES

I.C.1. FGM ASSAY

We assayed deer FGM in 205 fecal samples adapting the method described by Martin et al (2013) and Renaud (2012). A methanol-based protocol was used to extract fecal glucocorticoid metabolites (Brown et al. 2004). Feces were weighed in clean culture glass tubes (16 mm x 100

mm) to obtain $100 \text{ mg} \pm 10 \text{ mg}$ per sample, then 5 ml of 90% methanol were added to each sample. Tubes were vortexed at room temperature at 250 rpm for 4 hours and at 380 rpm for 35 minutes. Samples were filtered with a $0.45 \text{ }\mu\text{m}$ non-sterile filter fixed on a syringe and stored at -20°C to limit bacterial degradation until the assay of glucocorticoid metabolites.

Competitive enzyme-linked immunosorbent assays (ELISA) were performed in triplicate for each extract using a 96-well microtiter plate (Nunc-Immuno, Maxisorp Surface; Fisher Scientific, Pittsburgh, PA, USA). We used a polyclonal cortisol antibody (R4866, C. J. Munro, University of California, Davis, CA, USA) with the following cross-reactivity : cortisol, 100.00%; compound S, 6.21%; corticosterone, 0.75%; desoxycorticosterone, 0.14%; 17- α -hydroxy-progesterone, 0.09%; progesterone, 0.03%; testosterone $<0.01\%$; 17- β estradiol, $<0.01\%$; estrone, $<0.01\%$; androstenedione, 0.02%; and androsterone, $<0.01\%$ (Munro & Lasley 1988). Sensitivity of the cortisol polyclonal antibody was 0.3 pg/wells (Munro & Lasley 1988). The polyclonal cortisol antibody was diluted 1:10 000 in a commercial bicarbonate coating buffer (pH 9.6; ImmunoChemistry Technologies, Bloomington, MN, USA). We added $50 \text{ }\mu\text{l}$ of this solution to each well, except the blank, and incubated for 18 hours at 4°C . The next morning, plates were rinsed three times with wash buffer (NaCl, 0.15 M; 0.05% of Tween-20) and blocked. After a 2-hour incubation at 4°C , plates were rinsed five times with wash buffer.

To perform the assay, we added to the wells $50 \text{ }\mu\text{l}$ of assay buffer (NaH_2PO_4 0.65 M, Na_2HPO_4 1.03 M, NaCl 0.15 M, pH 7.0), $50 \text{ }\mu\text{l}$ of standards or samples and $50 \text{ }\mu\text{l}$ of horseradish peroxidase conjugate (cortisol -3-CMO) provided with the kit and previously diluted 1:50 000 in assay buffer. Standards (diluted cortisol solution; Sigma-Aldrich, St. Louis, MO) were assayed in duplicates in a range of 19.53 to 2500 pg/ml in assay buffer. After a 1-hour incubation at room temperature on an orbital shaker, plates were washed five times and $100 \text{ }\mu\text{l}$ of fresh substrate buffer (40 mM ABTS [2,2'-azino-bis (3-ethylbenzothiazoline-6- S ulphonic acid] diammonium salt, 1.6 mM H_2O_2 , 0.05 M citric acid pH 4.0) were added to each well. After a 40-minute incubation on an orbital shaker at room temperature, absorbance was read at 405 nm with a microplate spectrophotometer (Multiskan GO, Thermo Fisher Scientific Inc., Waltham, MA, USA). The assay was repeated for any sample in which triplicates differed by 20% or greater (Munro & Lasley

1988). FGM levels were calculated and expressed as a function of dry fecal mass (ng/g) for each sample.

I.C.2. ASSAY VALIDATIONS

Three technical validations of the quality of the assays were conducted as suggested by Buchanan and Goldsmith (2004): (i) we tested parallelism by pooling five pellets from different fecal samples which were then weighted and extracted together. We diluted the pool serially (1, 1:2, 1:4, 1:8, 1:16, 1:32, 1:64 and 1:128) to compare parallelism with the standard curve. Curves obtained with serially diluted extracts from the sample pool and with cortisol standards were parallel; (ii) we calculated repeatability by measuring FGM levels for six samples with seven or eight independent replicates. Average repeatability was 82% [95% CI: 60 ; 97]; (iii) we evaluated intra-assay coefficients of variation (CV) in two ways: using triplicates for each sample we estimated intra-assay CV to be on average $11.3 \pm 4.7\%$ (mean \pm sd) ; using a cortisol standard solution (1250 pg/ml) we estimated intra-assay CV to be on average $7.2 \pm 5.9\%$.

It was not logistically feasible to validate directly the relationship between plasmatic and FGM levels. However, this relationship had been validated with adrenocorticotrophic-hormone (ACTH) challenges for a large range of deer species [e.g. red (*Cervus elaphus*) and fallow deer (*Dama dama*): Bubenik & Bartos 1993; roe deer (*Capreolus capreolus*) : Dehnhard et al. 2001; reindeer (*Rangifer tarandus*) : Ashley et al. 2011] including white-tailed deer (*Odocoileus virginianus*: Millspaugh et al. 2002). Therefore, we considered that FGM levels adequately reflected black-tailed deer physiological stress levels.

I.D. NITROGEN ASSAY

We assessed the nitrogen content of 198 fecal samples (c. 6-12 samples/month/island). Elemental N content (%) was measured by dry combustion using an EA3000-IRMS elemental analyzer (Eurovector 2010) coupled to an Optima continuous flow mass spectrometer (Micrometer, ISEM Université de Montpellier II). We used IAEA-NO-3 (N%=13) as reference to assess the proportion of nitrogen in each sample. The analytical precision for nitrogen content in the NO-3 standard was c.1%. On inspection, levels of fecal nitrogen assessed were similar to

those reported in other deer species in temperate environments (Kucera 1997; Kamler & Homolka 2005; Miyashita et al. 2007; Christianson & Creel 2010; Verheyden et al. 2011).

I.E. MICRO-HISTOLOGICAL ANALYSES

We estimated seaweed consumption from a micro-histological study of 86 fecal samples (8-10 samples/island for June, October 2011 and March 2012). For each sample, we rehydrated five pellets with mild water over night. The next day we sieved these pellets at 0.2mm, rinsed them with water and soaked them in 2.6% sodium hypochlorite for 5 minutes. A fraction of the remaining epidermis was diluted in a drop of glycerin and examined under a binocular microscope at a magnification of 100x (see Poilvé 2013). We used a reference collection of plants collected on the studied islands to identify the origin of 100 epidermal fragments (seaweed, terrestrial plants, or unknown) randomly drawn from each sample. We then computed the proportion of seaweed fragments among the 100 fragments examined.

I.F. STATISTICAL ANALYSES

We assessed seasonal variations in FGM levels and nitrogen content among islands using linear models with log-transformed values for FGM and N content as response variables and the month, the island and their interaction as explanatory variables. We used Wald-test-based comparisons with Hommel's adjusted P-value to study the significance of pairwise differences among FGM levels and N content between months within each island and between islands for a given month (Hommel 1988; Fox & Weisberg 2011).

We studied the effect of seaweed consumption on FGM levels using a linear model with the log-transform value of FGM levels as the response variable and the proportion of seaweed, the month, the island and all possible interactions as explanatory variables. We identified significant effects using the residual sum of square-ratio tests on nested models (Fox & Weisberg 2011). In all analyses we accepted a 5% type I error. All analyses were run with the R software (R Core Team 2012) and the *car* package (Fox & Weisberg 2011).

II. RESULTS

II.A. SEASONAL VARIATIONS AND INTER-ISLAND DIFFERENCES IN FGM LEVELS

FGM levels ranged between 5.5 and 54.2 ng/g. Annual average levels were similar between the three islands (annual mean \pm sd: East Limestone = 20 ± 8 ng/g; Kunga: 19 ± 5 ng/g; Reef = 20 ± 4 ng/g). The three islands also presented similar seasonal trends, although of different magnitude (Figure II.1 a, Appendix II.A): FGM levels tended to increase between April and July by 182% on East Limestone ($X^2= 49.0$, $P < 0.001$), 68% on Kunga ($X^2=10.3$, $P=0.03$) and 25% on Reef ($X^2=2.1$, $P > 0.999$). FGM levels then decreased between July and October by 56, 49 and 39% on East Limestone ($X^2=34.4$, $P < 0.001$), Kunga ($X^2=17.5$, $P < 0.001$) and Reef ($X^2=12.8$, $P=0.009$), respectively, when they reached values similar to those observed at the end of the winter (March).

We found only few significant differences between monthly FGM levels among islands: in April, FGM levels on East Limestone (12 ± 3 ng/g) were almost half those observed on Reef (22 ± 5 ng/g) ($X^2=17.05$, $P=0.001$); in June, FGM levels on East Limestone were 1.6 times higher than those observed on Reef (East Limestone: 28 ± 6 ng/g; Reef: 17 ± 3 ng/g) ($X^2=9.72$, $P=0.04$). For all other comparisons $X^2 \leq 7$ and $P \geq 0.18$ (Figure II.1 a).

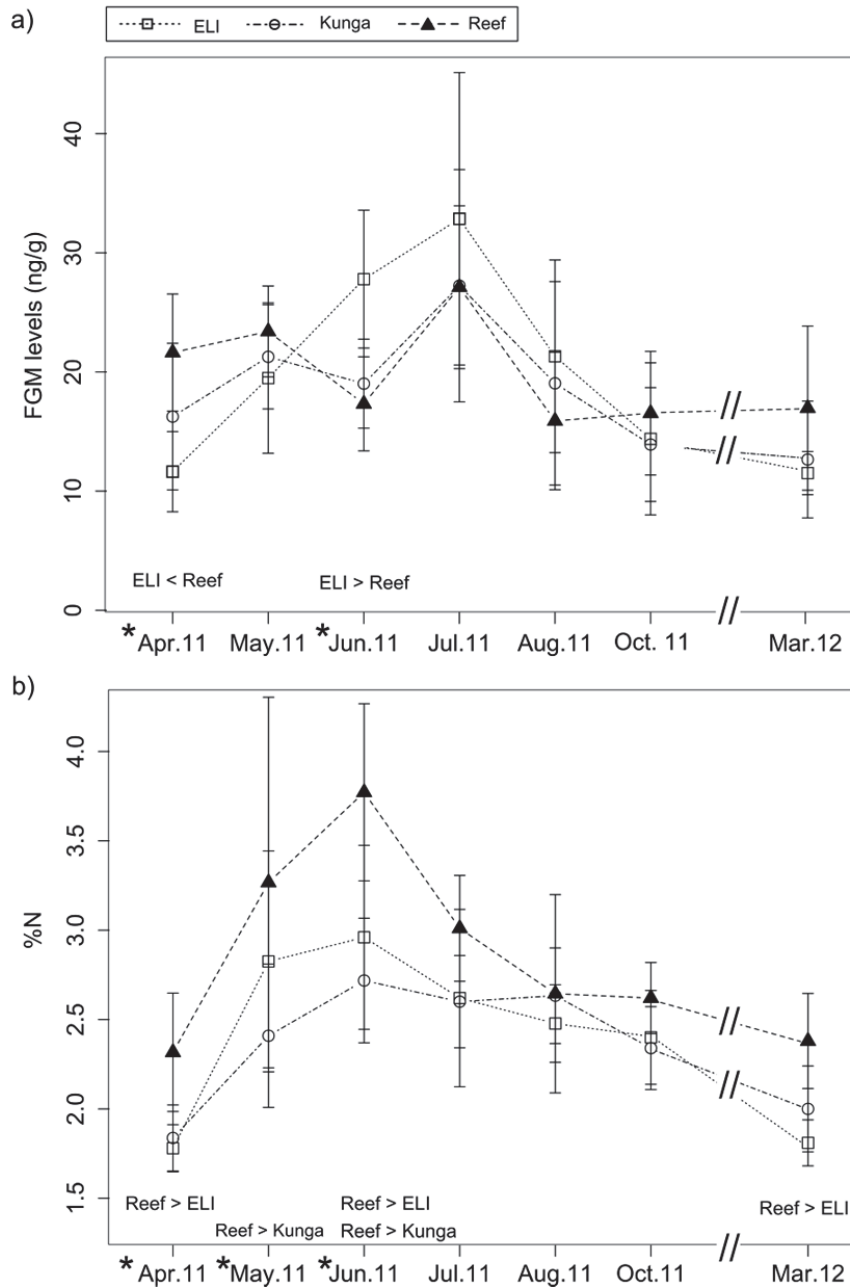


Figure II.1: Seasonal variation of fecal glucocorticoid metabolite (FGM) levels (a) and fecal nitrogen content (b) in black-tailed deer on three islands of the Haida Gwaii archipelago (East Limestone (ELI): square, Kunga: circle, Reef: triangle) in 2011-2012. We used open dots for predation-free islands with a depleted forest understory: (safe/poor islands: East Limestone and Kunga) and closed dots for the hunted island with a rich forest understory (risky/risk island: Reef). Months with significant differences among islands are identified by a star and the comparison is detailed above the x-axes. For each island, significant differences among monthly FGM levels and fecal nitrogen content are presented in Appendix II.B.

II.B. SEASONAL VARIATIONS AND INTER-ISLAND DIFFERENCES IN FECAL NITROGEN CONTENT

Fecal nitrogen content ranged between 1.6 and 5.2%. On the three islands fecal nitrogen increased during spring (April vs. June : East Limestone: $X^2=23.9$, $P<0.001$; Kunga: $X^2=32.4$, $P<0.001$; Reef: $X^2=40.8$, $P<0.001$) and then decreased continuously until the end of winter (June vs. March: East Limestone: $X^2=53.8$, $P<0.001$; Kunga: $X^2=22.7$, $P<0.001$; Reef: $X^2=40.2$, $P<0.001$) (Figure II.1 b). As expected, and more noticeably in spring and late winter, fecal nitrogen was higher by c. 0.5-1% on Reef than on East Limestone (East Limestone vs. Reef in March, April and June: $X^2>11$; $P<0.02$) and on Kunga (Kunga vs. Reef in June and May: $X^2>16$, $P<0.001$). All other comparisons inter-island had $X^2<8$ and $P>0.11$. In particular, Kunga and East Limestone showed similar levels of nitrogen content throughout the year ($X^2<5$ and $P>0.5$ for all months).

II.C. EFFECT OF SEAWEED ON FGM LEVELS

Seaweed epidermis was present in 38% of the fecal samples analyzed, and when present seaweeds never represented more than 13% of the 100 epidermal fragments analyzed per feces. Feces that did contain seaweeds mostly came from Kunga (64%). There was no relationship between the proportion of seaweeds found and the FGM levels (Table II.1).

Table II.1: Statistical models to test the effect of seaweed on fecal glucocorticoid metabolite (FGM) levels in black-tailed deer during three months (June, October and March) on three islands of the Hadai Gwaii archipelago (East Limestone, Kunga and Reef). Significant effects are detected by comparing the residual sum of square (RSS) of the reference model (which included the effect tested) with the focus model (which did not include this effect).RSS, F-statistics and P-values are presented. Significant effects are in bold.

Explanatory variable	Reference model	RSS reference model	RSS focus model	F	P
%seaweed x month x island	Model with 3- and all 2-way interactions and main variables	7.119	7.348	0.738	0.533
%seaweed x island			7.429	0.398	0.673
%seaweed x month	Model with all 2-way interactions and main variables	7.348	7.738	1.911	0.155
month x island			8.615	3.105	0.020
%seaweed	Model with significant 2-way interactions and main variables	7.856	7.931	0.729	0.396

III. DISCUSSION

III.A. FGM LEVELS AND RELATIVE EFFECTS OF LOW FOOD ABUNDANCE AND PREDATION RISK

FGM levels fell within a range of c. 10-35 ng/g (Figure II.1 a). Comparisons with other studies are limited due to differences in the methods used (Millspaugh & Washburn 2004). It seems that deer did not mount a strong stress response to the presence of a prolonged-exposure to low food abundance or predation risk. Indeed, the FGM levels in our study were similar to or in the lower range of those reported for captive deer protected from most stressors (predation, food shortages), such as in hand-raised white tailed deer (c. 11–90 ng/g : Washburn & Millspaugh 2002; Millspaugh & Washburn 2003; Moll et al. 2009) or in reindeer (*Rangifer tarandus*) (c. 34-49 ng/g: Ashley et al. 2011). They also fell within the range of FGM levels reported for free-ranging elk (*Cervus elaphus*) exposed to seasonal changes in food levels, temperatures, hunting and tourist activities in South Western Dakota, US (c. 10-45 ng/g: Millspaugh et al. 2001). The observed FGM levels were, however, much lower than the FGM levels reported for deer exposed to predation risk and human activities and possible food limitation ([FGM] > 800 ng/g in wintering elk : Creel et al. 2002; [FGM] > 150 ng/g in pampa deer (*Ozotoceros bezoarticus*) : Pereira et al. 2006). The observed FGM levels were also much lower than those reported for deer following an injection of adrenocorticotrophic hormone (ACTH challenge) which promotes the release of glucocorticoids (e.g. [FGM] > 130 ng/g: Washburn & Millspaugh 2002; Millspaugh & Washburn 2003; Ashley et al. 2011) (Appendix II.B). We found no relationship between seaweed consumption and FGM levels, and thus ruled out that these marine subsidies could bias the comparisons

FGM levels were globally similar between the three islands despite contrasted situation in food abundance and predation risk (Figure II.1 a). How much risk is actually perceived by deer in each situation could not be assessed directly. However, the fact that winter energy balance is negative in deer on East Limestone and Kunga (Chapter I) and that deer seem to avoid humans on Reef, strongly suggests that deer should perceive some level of risk and hence seem to cope similarly with both stressors, at least physiologically. This supports Clinchy et al's (2004) study that reported similar basal glucocorticoid levels in song sparrows exposed to either starvation or

predation risk. The natural setting of our study prevents to assess whether changes in the levels of food abundance and predation risk would affect deer stress response similarly. However, it would be interesting to compare the relative effect of gradients of food abundance and predation risk on animal stress response in other systems. For example, comparing the magnitude of change in deer stress response caused by either supplementary winter food supply (reduction in starvation risk) or by increasing human activities (increase in predation risk) could shed light on the relative flexibility of deer stress responses to different risk gradients. This could also be complemented by other physiological metrics (e.g. metabolic rate, oxidative stress) which might help to better assess the intensity of energy stress perceived by deer (e.g. review in Hawlena & Schmitz 2010; Clinchy et al. 2013).

In addition, individuals may use different behavioral and/or physiological strategies to cope with a given stressor (Travers et al. 2010; Homyack 2010; Clinchy et al. 2011, 2013) or different ones (Wingfield 2008). In particular, it would be interesting to investigate whether deer response to an acute stressor (e.g. predator cues, handling) would be similar among these contrasted risk regimes. Indeed, Hanlon et al. (1995) showed that elk subjected to social stress (group mixing) had similar basal glucocorticoid levels than elk in control groups (no change in group composition) but stressed elk mounted higher stress response to ACTH challenge than control elk. This pattern highlight the main difference between basal levels of glucocorticoids, which reflect the overall energy requirements of an organism over a given period, and stress response to an acute stressor (e.g. ACT challenge) which inform on the immediate ability of an individual to cope with an unpredictable short-term stressor (e.g. conspecific aggression, predator encounter, climatic conditions) (Sapolsky et al. 2000; Romero 2004; Wingfield 2005). Because both glucocorticoid baseline and stress response to an acute stressor may affect individual fitness (Angelier & Wingfield 2013), a comprehensive comparison of the effect of a prolonged-exposure to either low food abundance or predation risk would require complementing the present study by assessing animal response to acute stressors.

III.B. RESPONSES TO SEASONAL CHANGES IN FOOD ABUNDANCE AND PREDATION RISK

Surprisingly, although we expected deer on different islands to respond differently to seasonal contrasts in food availability (winter vs. summer) and in human activities (research activity in spring and fall) likely perceived as perturbation (on East Limestone) or predation risk (on Reef), this was not the case (Appendix II.A). Seasonal FGM patterns were similar on the three islands irrespective of their long-term low food abundance or predation risk regimes. We interpreted this discrepancy between risk regimes and stress responses as the result of a modulation of the energy demand made possible by behavioral and/or physiological adjustments.

First, regarding winter starvation risk on East Limestone and Kunga, FGM levels did not increase in winter or early spring but were instead lower than in late spring -summer when resources were more abundant (Appendix II.A.1, II.A.2). This result was even more striking as fecal nitrogen content, an index of deer diet quality, was, as expected, lower in winter – early spring than in late spring-summer (Figure II.1 b) and that deer energy balance was likely to be negative in winter (Chapter I). However, deer are known to reduce their activity rate in winter when resources are scarce and/or climatic conditions rigorous (e.g. Beier & McCullough 1990; Parker et al. 1999; Zhang 2000; Pépin et al. 2009; Massé & Côté 2013). East Limestone and Kunga deer indeed reduced their activity budget by c.10-20% in late winter-early spring (December to April) when compared to the spring-summer (May to September) (unpublished data from activity-sensors). Such behavioral changes may reduce deer energy demand (Parker et al. 1999) associated with reduced winter metabolism and lower glucocorticoid levels, as observed in white-tailed deer (DelGiudice et al. 1992). In addition, deer may also be able to cope with severe food restriction by reducing their glucocorticoid levels. This was reported by Taillon & Côté (2008) in white-tailed deer on Antiscoti Island (Q.C., Canada), where fawns fed with an impoverished diet in winter presented lower FGM levels than fawns fed with a normal diet. Taillon & Côté (2008) suggested that when individual body condition was too low to mount a full stress response, individuals may reduce glucocorticoid levels and suppress their stress response thus reducing the deleterious impact of chronic stress. This would possibly explain why in late winter/early spring 2012 deer on East Limestone had lower FGM levels than deer on Reef despite a stronger winter food restriction (Figure II.1 a).

Second, FGM levels did not increase consistently during the months with human activities on Reef. In particular, they were not higher in October, when researchers were on the island, than in August when they were not. (Figure II.1 a, Appendix II.A.3). This suggests that either deer did not perceive risk in the presence of humans or that deer behave in a way so that there was no need for them to mount a stress response. Whether non-hunting humans were actually perceived as a threat by deer on Reef cannot be tested directly. However, deer were rarely seen by humans, despite a density estimated to be 17 deer/km² (c. 40 deer, [95% CI: 24; 72], unpublished data), and there was evidence of higher nocturnal activity of deer in areas most commonly used by people (unpublished camera trap data and pers. obs.). This suggests that deer of the study avoid human presence and areas considered unsafe, as found commonly elsewhere (e.g. Kilgo et al. 1998; Creel & Winnie Jr. 2005; Proffitt et al. 2009; Bonnot et al. 2013). This risk-avoidance has been suggested as a behavioral adjustment to limit physiological stress in an elk population in which glucocorticoid levels were found to be independent from wolf predation risk (Creel et al. 2009). Thus, the absence of stress response in the presence of human activities may be explained by behavioral adjustments.

Remarkably, FGM levels were higher in spring- summer than in fall or winter on the three islands. High FGM levels in spring/summer are likely to be linked to the high energy demand for antler growth in males (Pereira et al. 2006; Gaspar-López et al. 2010) and for gestation and early lactation in females (Sadleir 1982; Bowyer 1991; DelGiudice et al. 1992; Keay et al. 2006). Changes in FGM levels on East Limestone were more pronounced than on Kunga or on Reef. Group of 3-6 research volunteers worked on East Limestone from May to June and their presence has been found to be correlated with higher diurnal vigilance levels in deer (Chapter III). This suggests that deer on East Limestone may perceive humans as disturbing agents or threats. Human presence combined to the energy demand due to reproduction might explain the high FGM levels observed on East Limestone in June. East Limestone is six times smaller than Reef and deer are at least 3 times more abundant (Chapter I). Contrary to deer on Reef, deer on East Limestone may thus have limited alternatives to avoid human activities and hence may not be able to respond behaviorally (space use) to humans as much as deer on Reef.

To conclude, we showed that under contrasted risk situations with prolonged exposure to either food restriction or to predation risk, deer presented similar FGM levels. Similar seasonal variations also occurred in deer FGM levels with a marked increase during late spring/summer simultaneous to reproduction. Unexpectedly, FGM levels increased neither with a seasonal increase in food shortages nor with an increase in predation risk induced by human presence. We interpreted this result as the consequence of behavioral and/or physiological adjustments that mitigate the levels of risk perceived by deer to allow them to cope with perturbations without mounting strong and prolonged stress response. Our results could be broadened by considering other measures of physiological stress (e.g. metabolic rate) and studies that explore the ability of deer to respond to gradients of risk and to acute stressors.

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APPENDIX II.A. SEASONAL VARIATIONS OF FECAL GLUCOCORTICOID METABOLITE LEVELS AND FECAL NITROGEN CONTENT PER ISLAND

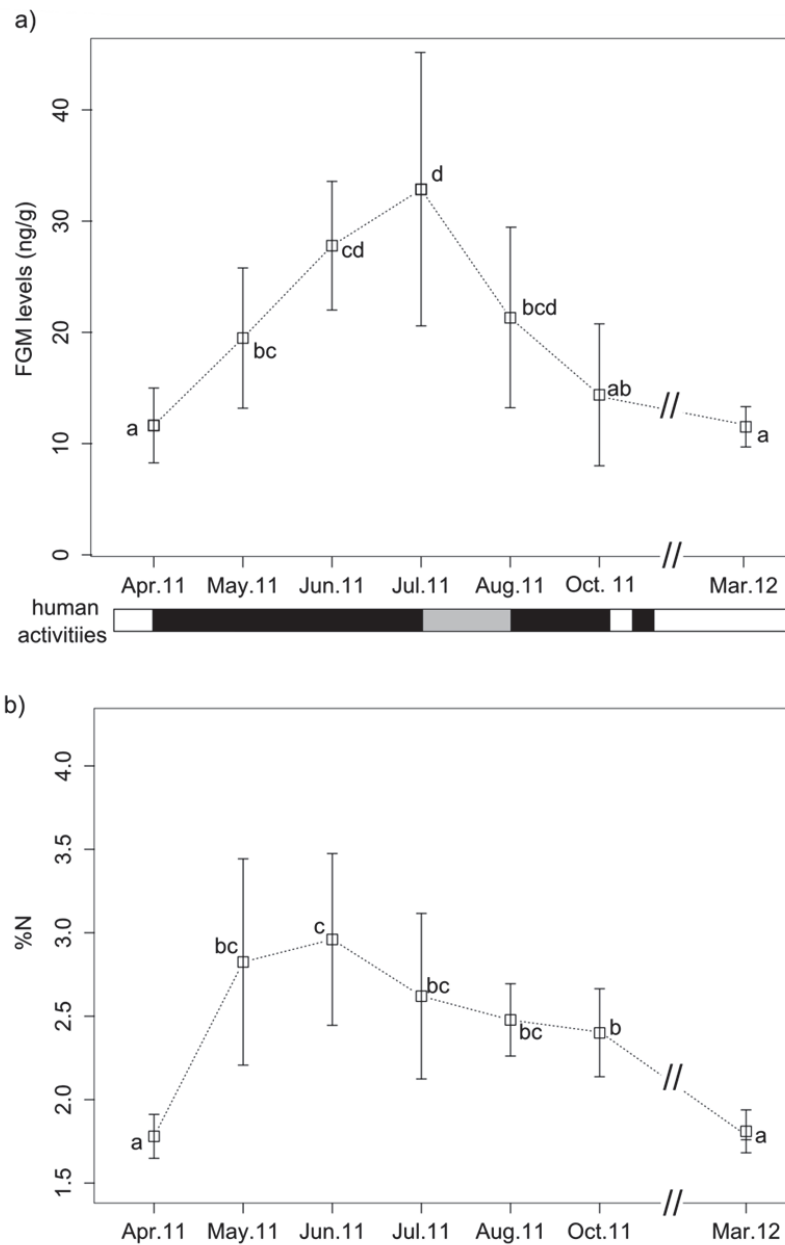


Figure II.A.1: Seasonal variations of fecal glucocorticoid metabolite (FGM) levels (a) and fecal nitrogen content (b) on East Limestone (safe/poor island). Months with human activities are highlighted in black for research activities and in grey for possible occasional tourist visits. Letters identify significant different levels among months. Mean values \pm standard errors are presented.

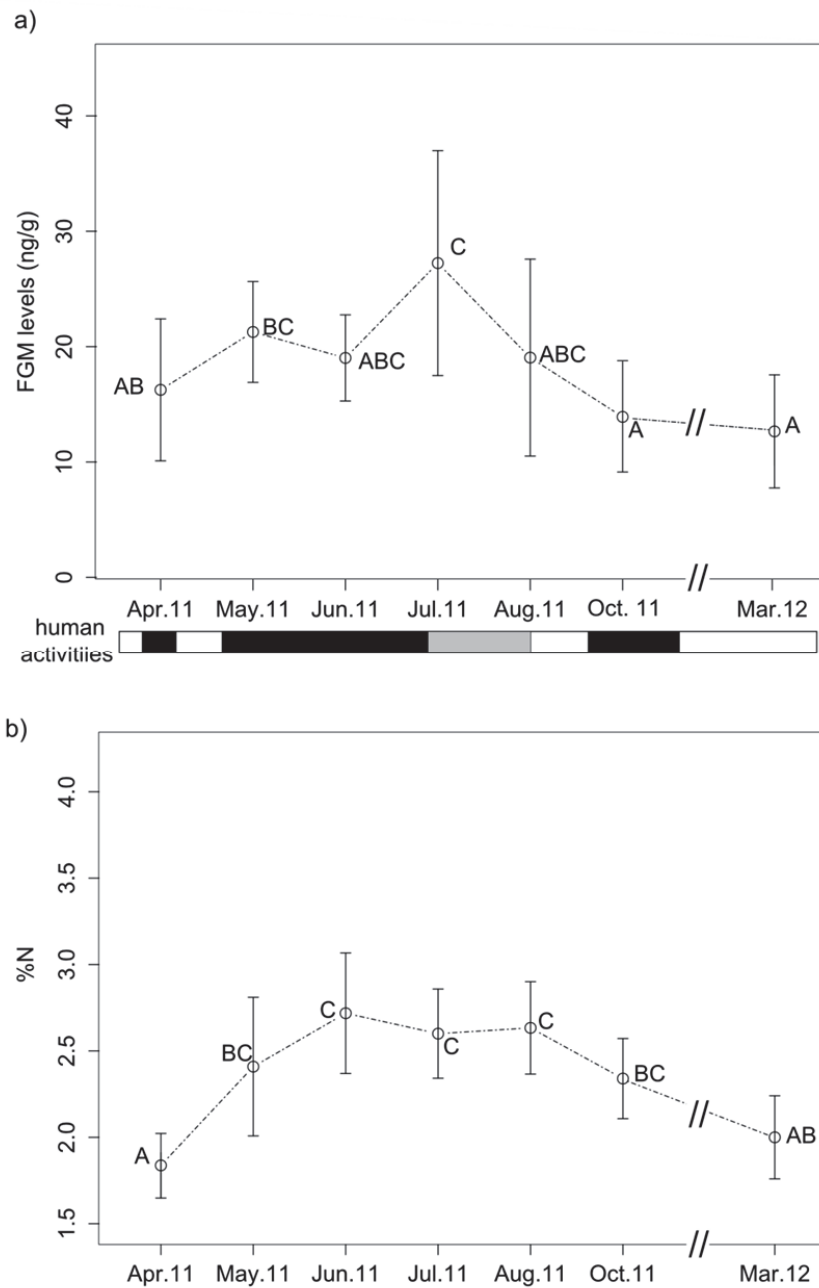


Figure II.A.2: Seasonal variations of fecal glucocorticoid metabolite (FGM) levels (a) and nitrogen content (b) on Kunga (safe/poor island). Months with human activities are highlighted in black for research activities and in grey for possible occasional tourist visits. Letters identify significant different levels among months. Mean values \pm standard errors are presented.

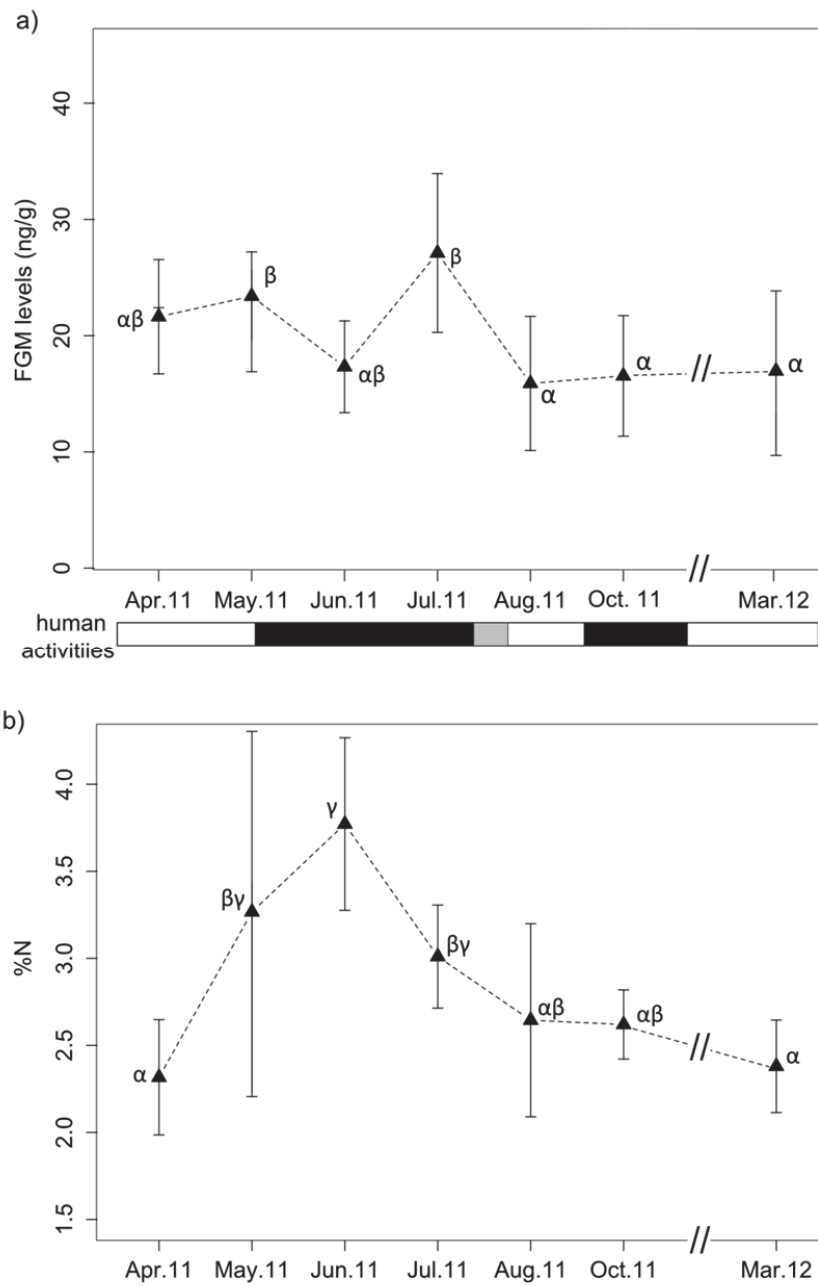


Figure II.A.3: Seasonal variations of fecal glucocorticoid metabolite (FGM) levels (a) and nitrogen content (b) on Reef (risky/rich island). Months with human activities are highlighted in black for research activities and in grey for occasional tourist visits. Letters identify significant different levels among months. Mean values \pm standard errors are presented.

APPENDIX II.B. PUBLISHED FECAL GLUCOCORTICOID METABOLITE LEVELS MEASURED IN DEER

We restricted our review to measurements of fecal glucocorticoid metabolite (FGM) levels assayed with either cortisol or corticosterone radio- or enzyme- immunoassay kits. Assay for a single (e.g. 11-oxoetiocholanolone) or a couple glucocorticoid metabolites (e.g. 11,17-dioxoandrostanes, 3 α -11-oxo cortisol metabolite) were not considered in this comparison.

Species	Environment : - food - predation, human activities	Hormone assay kit	FGM levels: range of mean values and/or mean values (ng/g)	Ref.
<i>Cervus elaphus</i>	- Food: seasonal changes - Hunting, tourist activities	125I corticosterone radioimmunoassay kit	range: c. 10-45 mean: c. 17 ; 34	1
<i>Cervus elaphus</i>	- Winter food deprivation - Wolves present, tourist activities	125I corticosterone radioimmunoassay kit	range: c. 800-2000	2
<i>Odocoileus virginianus</i>	Fed captive deer in outdoor facility (sampling conditions)	125I corticosterone radioimmunoassay kit	range: c.40 – 115	3
<i>Odocoileus virginianus</i>	Fed captive deer in outdoor facility	125I corticosterone radioimmunoassay kit	<u>Before ACTH challenge:</u> range : c. 40-90 <u>After ACTH challenge :</u> range c. 140-225	4
<i>Odocoileus virginianus</i>	Fed captive deer in outdoor facility (sampling conditions)	125I corticosterone radioimmunoassay kit	<u>Before ACTH challenge:</u> range : c. 60-70 <u>After ACTH challenge :</u> mean c. 130	5
<i>Odocoileus virginianus</i>	- Winter food deprivation and depleted diet - Protected from hunting	125I corticosterone radioimmunoassay kit	range: c. 40 – 130 mean: c. 62; 70	6
<i>Odocoileus virginianus</i>	Fed captive deer	125I corticosterone radioimmunoassay kit	range : c. 11-18	7
<i>Ozotoceros bezoarticus</i>	- Food: seasonal changes - Cougar present, no hunting, tourist activities	Cortisol enzyme immunoassay kit	range : c. 150 – 350	8
<i>Rangifer tarandus</i>	Fed captive reindeer	125I corticosterone radioimmunoassay kit	<u>Before ACTH challenge:</u> range: c. 34 -49 <u>After ACTH challenge:</u> range : c. 133 – 142	9
<i>Odocoileus hemionus</i>	- Food: poor vs. rich - Hunting: absent vs. present, tourist and research activities	Cortisol enzyme immunoassay kit	range: c. 10-35 mean: c. 20	10

References : 1 (Millspaugh et al. 2001), 2 (Creel et al. 2002), 3 (Washburn & Millspaugh 2002), 4 (Millspaugh et al. 2002), 5 (Millspaugh & Washburn 2003), 6: (Taillon & Côté 2008), 7: (Moll et al. 2009), 8: (Pereira et al. 2006), 9 (Ashley et al. 2011), 10 current study

COMPLEMENTARY ANALYSIS II

INVESTIGATING THE EFFECT OF SEAWEED CONSUMPTION ON DEER GLUCOCORTICOID LEVELS: DO CARBON AND NITROGEN ISOTOPES HELP?

Isotopes are atoms with the same number of electrons and protons but different numbers of neutrons (Sulzman 2008). Isotopes of a given chemical elements have thus slightly different mass according to the difference in the number of neutrons. The lighter, the more stable and hence the more common the isotope is (i.e. stable isotopes are c. 20 times more abundant than other forms: Fry 2006 in Inger & Bearhop 2008). Although isotopes have globally similar properties, this slight difference in mass is responsible for slight differences in chemical (e.g. reaction speed, boiling point) and physical properties (e.g. diffusion) (Peterson & Fry 1987; Sulzman 2008). Thus, the ratio between heavy and light isotopes (R) varies as function of the source and the process considered. A change in isotopic ratio during a process is called fractionation. For comparison reason, isotopic ratios are standardized and referred as δ , the part per thousand deviation of a given sample to the standard (Equation CA.II.1).

$$\delta = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (\text{Equation CA.II.1})$$

Terrestrial and marine habitats have different chemical and physical properties and hence present different isotope signatures (Peterson & Fry 1987). In particular, terrestrial and marine plants have access to different sources of carbon (terrestrial: atmospheric CO₂; marine: HCO₃⁻, CO₃²⁻ and CO₂ for intertidal plants) and nitrogen (terrestrial: NH₄⁺, NO₃⁻ and atmospheric N₂ for microbial fixation; marine: dissolved N₂ and NO₃⁻ in deep water) and use different processes to assimilate them (e.g. different photosynthesis, nitrogen assimilation) (e.g. review in Peterson & Fry 1987; Maberly et al. 1992; Inger & Bearhop 2008; Marshall et al. 2008). Terrestrial and marine plants may thus present different C and N isotopic signatures.

Similarly, from an animal point of view, the isotopic composition of its food (source) is correlated to the isotopic composition of its tissue (e.g. muscle, bones, feather, hair) and excreta (urine and feces) (e.g. C isotope: DeNiro & Epstein 1978; N isotope: Sponheimer et al.

2003c). “Animals are what they eat” (Inger & Bearhop 2008) and tissues and excreta are “dietary archives” (Sponheimer et al. 2003a). Therefore, a large body of science used isotopic values to assess animal use of terrestrial and marine resources (e.g. Walker & Deniro 1986; Ramsay & Hobson 1991; Stapp et al. 1999; Balasse et al. 2005, 2009).

However, isotopic analyses are relevant to discriminate the consumption of different food items only if the difference among food items is larger than the one within similar food items (Peterson & Fry 1987; Inger & Bearhop 2008). $\delta^{13}\text{C}$ is globally consistent over terrestrial plant species and varies by c. 2‰ among different environment (e.g. soil, climate) (Codron et al. 2005a). However, $\delta^{15}\text{N}$ in terrestrial plants is sensible to local environment (e.g. rainfall, salinity) and may vary up to 4‰ among different localities for a single species (Heaton 1987). Similarly, although $\delta^{13}\text{C}$ may vary by c. 5‰ over seaweed species (Raven et al. 2002), $\delta^{13}\text{C}$ is globally more stable within seaweed species than $\delta^{15}\text{N}$ which is more affected by local environmental conditions (e.g. upwellings) (Marconi et al. 2011). Using isotopic signatures as a dietary proxy requires thus preliminary validations.

Here, we investigated if, given the data available, we could use fecal $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$ as a proxy of seaweed consumption by deer in the study sites. If yes, we would be able to interpret the correlation between fecal isotopic signatures and fecal glucocorticoid metabolite concentrations in terms of seaweed consumption. If not, we would identify gaps in our data and suggest some recommendations for future study, at least in our study area.

I. MATERIAL & METHODS

I.A. AVAILABLE DATA AND METHODOLOGY

For this exploratory analysis, we had access to: (1) published dataset on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of terrestrial and marine plants; (2) a limited dataset with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for 20 plant species sampled on Graham Island and nearby islands (within c. 50 -100 km from the study islands, Figure CA.II.1) (3) a more detailed dataset (A. Salomon’s pers. comm.) with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for nine seaweed genus sampled offshore Louise and Lyell Island (within 1-30 km from the study islands, Figure CA.II.1); and (iv) 198 fecal samples for which glucocorticoid metabolite

concentration and/or micro-histological composition were known and for which $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were assessed.

First we combined the three datasets on plant isotopic signatures to assess whether terrestrial plants and seaweed presented contrasted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges. This is a necessary prerequisite to use isotopic signatures as dietary proxy (Peterson & Fry 1987; Inger & Bearhop 2008). Secondly, when relevant we investigated the correlation between $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$ values and the micro-histological composition of a given fecal sample. Interpretations were conducted in the light of micro-histological analyses conducted by Poilvé (2013). Thirdly, if relevant, we would study the relationship between glucocorticoid and $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$ values for a given sample and interpret it in relation to seaweed consumption.

1) Literature review and estimation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges of terrestrial plants and seaweeds in the study area.

For terrestrial plants, we focused on C3 plants, since to our knowledge C4 plants do not occur on the study island (Pojar & MacKinnon 1994). We used Bender (1971), Peterson & Fry's (1987), Cerling & Harris's (1999) and Balasse et al.'s (2005) studies to assess the range of $\delta^{13}\text{C}$ in C3 plants. For $\delta^{15}\text{N}$ values we used Heaton's (1987) and Peterson & Fry's (1987) studies. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges were estimated by the minimum and maximum average values reported for C3 plant species.

For seaweed, we considered only genus that were identified as candidate food items for deer on the study islands: i.e. *Alaria*, *Costaria*, *Cymathere*, *Egregia*, *Fucus*, *Hedophyllum*, *Laminaria*, *Macrocystis*, *Nereocystis*, *Pleurophyucus* for brown algae and *Halosaccion*, *Porphyra* *Palmaria* and *Rhodymenia* for red algae (pers. obs.). We used Maberly et al.'s (1992), Raven et al.'s (2002) and Marconi et al.'s (2011) studies to assess $\delta^{13}\text{C}$ range and Marconi et al.'s (2011) study to assess $\delta^{15}\text{N}$ range. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges were estimated by the minimum and maximum average values reported for the considered seaweed species.

2) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for some plant samples from Graham Island and nearby islands

In December 2010, we collected a single to three samples for 20 plant species including: four fern, two grass, four shrub, five tree, four lichen and a seaweed species (Table CA.II.1). Collections took place on Graham, Burnt and Legace islands within c. 50 -100 km from the study islands, Figure CA.II.1. Samples were oven-dried at c. 50°C for 2 to 4 days (until their dry-mass was stable) and stored in paper envelopes until isotopic assay. Isotopic assay were conducted in February 2011, at Université Montpellier II (see below).

Table CA.II.1: Isotopic values for 20 plant species collected on Graham Island and nearby islands. Guild, species, sample size (n), sampling locality (1: Burnt Island, 2: Legace Island, 3: site 1 on Graham Island, 4: site 2 on Graham Island; Figure CA.II.1) and isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) are provided.

Guild	Latin name	n	Locality	$\delta^{13}\text{C}$ range	$\delta^{15}\text{N}$ range
fern	<i>Athyrium filix femina</i>		1	-30.77	1.03
fern	<i>Blechnum spicant</i>	1	3	-33.24	-5.05
fern	<i>Polypodium glycyrrhiza</i>	1	1	-32.06	-1.12
fern	<i>Polystichum munitum</i>	3	1	[-32.76; -30.6]	[-0.64; 0.38]
grass	<i>Carex sp</i>	1	1	-33.53	-2.15
grass	<i>Luzula sp</i>	1	1	-33.78	-1.54
lichen	<i>Alectoria sp</i>	1	3	-23.19	NA
lichen	<i>Liverwort sp.</i>	1	1	-28.37	-2.45
lichen	<i>Lobaria sp ?</i>	1	1	-32.42	-3.29
lichen	<i>Plastimatia sp ?</i>	1	1	-24.99	-6.73
shrub	<i>Gaultheria shallon</i>	3	3,4	[-31.07; -27.57]	[-12.80; -5.80]
shrub	<i>Ledum groenlandicum</i>	1	4	-29.42	-8.43
shrub	<i>Rosa nutkana</i>	1	4	-24.41	-2.49
shrub	<i>Vaccinium sp.</i>	1	1	-35.36	-2.39
tree	<i>Picea sitchensis</i>	2	4	[-29.23;-28.91]	[-4.94;-3.77]
tree	<i>Pinus concerta</i>	1	3	-30.58	-11.23
tree	<i>Salix sp</i>	1	2	-30.70	-8.37
tree	<i>Thuja plicata</i>	2	1,4	[-29.23.-27.80]	[-11.68. -9.09]
tree	<i>Tsuga hetetophylla</i>	2	4	[-33.49.-33.54]	[-11.74.-14.64]
brown alga	<i>Fucus sp</i>	2	2	[-18.69; -20.74]	[6.18; 6.67]

3) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for seaweeds from Louise and Lyell islands

In 2011, Salomon et al. collected and assessed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in 177 samples of nine seaweed genus (Table CA.II.2). Sampling took place offshore Louise and Lyell islands (Figure CA.II.1).

Table CA.II.2: Isotopic values for nine seaweed genus (Salomon et al.). Guild, species, sample size (n), sampling locality (5: Louise island, 6: Lyell island; Figure 1) and isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) are provided.

Guild	Latin name	n	Locality	$\delta^{13}\text{C}$ range	$\delta^{15}\text{N}$ range
Brown alga	<i>Alaria marginata</i>	27	5,6	[-24.79; -14.47]	[4.02; 7.96]
Brown alga	<i>Costaria costata</i>	29	5,6	[-25.74; -14.07]	[5.68; 9.18]
Brown alga	<i>Cymathaere triplicata</i>	26	5,6	[-23.32; -13.44]	[5.27; 8.75]
Brown alga	<i>Hedophyllum sessile</i>	25	5,6	[-20.86; -13.82]	[5.85; 8.46]
Brown alga	<i>Laminaria bongardiana</i>	8	5,6	[-21.49; -15.74]	[2.23; 7.1]
Brown alga	<i>Laminaria setchellii</i>	7	5,6	[-16.15; -13.55]	[5.15; 6.19]
Brown alga	<i>Macrocystis pyrifera</i>	22	5,6	[-19.02; -11.46]	[5.61; 9.59]
Brown alga	<i>Nereocystis luetkeana</i>	28	5,6	[-23.43; -13.59]	[5.24; 8.11]
Brown alga	<i>Pleurophycus gardneri</i>	4	6	[-21.39; -16.22]	[4.37; 6.68]
Brown alga	<i>Pterygophora californica</i>	1	6	-15.05	6.41

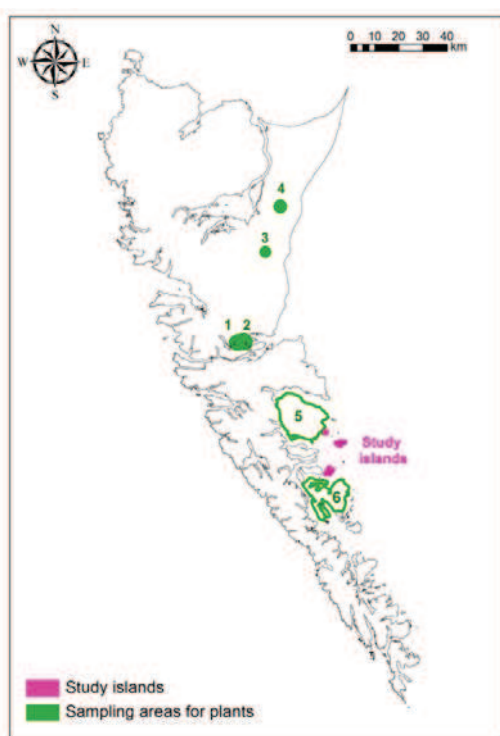


Figure CA.II.1: Localities on the Haida Gwaii archipelago where samples of terrestrial plant and seaweed were collected for isotopic analyses. The study islands are in purple and the sampling areas for terrestrial plants and seaweed are in green. Sampling areas are identified as follow: 1: Burnt Island, 2: Legace Island, 3: site 1 on Graham Island; 4: site 2 on Graham Island; 5 Louise Island; and 6: Lyell Island.

4) Fecal samples and isotopic assay.

We assessed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for 97% of the fecal samples (n=198) for which glucocorticoid levels were assayed. Among them, 46% (n=85) had micro-histological composition. The remaining and untouched dry matter of fecal samples were re-grinded and sieved at 125 μm . $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios were measured in a microgram of each homogenized remaining sample by dry combustion using a Euro Vector 3000 Elemental Analyzer coupled with a Micromass Optima Isotope Ratio Mass Spectrometre (ISEM, Université de Montpellier 2). The $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios were then expressed as δ values in parts per thousands (‰) relative to the Vienna-Pee Dee Belemnite and air nitrogen standards for carbon and nitrogen ratios, respectively. The standard deviation of replicate measurements of an internal standard was estimated to be 0.2‰ for carbon and nitrogen values.

I.B. ANALYSIS

I.B.1. $\delta^{13}\text{C}$ AND $\delta^{15}\text{N}$ RANGES IN TERRESTRIAL PLANTS VS. SEAWEED

To compare the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for terrestrial plants and seaweed we plotted on a one-dimensional axis the ranges assessed for each plant dataset (i.e. literature review, plant samples from Graham Island and nearby islands and A. Salomon's dataset). We examined these range in relation to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values assessed for fecal samples. We corrected fecal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values by -1‰ and -3‰, respectively, to account for isotopic fractionation when food is processed by herbivores (Ambrose & DeNiro 1986; Sponheimer et al. 2003a, 2003b)

I.B.2. CORRELATION BETWEEN ISOTOPIC VALUES AND MICRO-HISTOLOGICAL COMPOSITION

When relevant, we studied the correlation between the $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$ values and the micro-histological composition of fecal samples. We considered nine exclusive micro-histological classes: monocotyledon (unidentified grasses and forbs), dicotyledon (unidentified shrubs, forbs and trees), Sitka spruce, redcedar, western hemlock, fern, seaweed, other (e.g. seed, apple), and unknown. For each micro-histological class we conducted Spearman's test on the ranks obtained for each fecal sample according to either its isotopic value ($\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$) or its contents in the component considered (proportion of the micro-histological class). Results were

interpreted in the light of deer diet composition estimated from micro-histological analyses (Poilvé 2013).

I.B.3. CORRELATIONS BETWEEN ISOTOPIC VALUES AND GLUCOCORTICOID LEVELS

If relevant, we would study the relation between $\delta^{13}\text{C}$ (resp. $\delta^{15}\text{N}$) values and glucocorticoid levels in each sample by building a linear model with the log-transformed value of the fecal glucocorticoid metabolite concentration as the response variable and $\delta^{13}\text{C}$ (resp. $\delta^{15}\text{N}$) values, month, island and all interactions as explanatory variables. We would identify significant effects using the residual sum of square-ratio tests on nested models. For significant categorical variables or interaction with a categorical variable we would compare pairwise differences among the months within each island and between islands for a given month. If relevant, we would use Wald-test-based comparisons with Hommel's adjusted P-value to study the significance of these pairwise differences (Hommel 1988; Fox & Weisberg 2011). We would accept a 5% type I error.

All analyses were conducted with R software (R Core Team 2012) and the *car* package (Fox & Weisberg 2011)

II. RESULTS & DISCUSSION

II.A. $\delta^{13}\text{C}$ AND $\delta^{15}\text{N}$ RANGES IN TERRESTRIAL PLANTS AND SEAWEEDS IN RELATION TO THE ISOTOPIC SIGNATURE OF FECAL SAMPLES

$\delta^{13}\text{C}$ values were globally consistent among the three datasets: terrestrial plants had overall lower $\delta^{13}\text{C}$ values ($< -22\text{‰}$) than brown and red algae which had $\delta^{13}\text{C}$ values $> -22\text{‰}$ except for four brown algae in A. Salomon's dataset (Figure CA.II.2b A) and two red algae samples reviewed in Marconi et al. (2011) (one from New Zealand and one from Italy, Figure CA.II.2 A). This suggests that globally $\delta^{13}\text{C}$ values are different between terrestrial and marine plants. $\delta^{13}\text{C}$ values may thus inform on the proportion of seaweed in animal diet, as conducted in sheep by Balasse et al. (2005, 2006, 2009). However, we noted that $\delta^{13}\text{C}$ ranges assessed for deer fecal samples on the study islands were relatively low (average range for monthly $\delta^{13}\text{C}$ values corrected for fractionation in ‰: East Limestone: [-29.44;-28.16]; Kunga: [-28.97; -27.2];

Reef: [-30.17;-29.04] Figure CA.II.2 C). This suggested that seaweed may have a limited contribution in fecal isotopic signature what would limit the use of $\delta^{13}\text{C}$ values as a proxy for seaweed consumption.

$\delta^{15}\text{N}$ values were consistent among the three dataset for seaweeds but not for terrestrial plants (Figure CA.II.2 B). Brown and red algae had $\delta^{15}\text{N}$ values comprised between 2 and 10‰. C3 plants in the literature had value between -5 and 10‰ but values assessed on Graham Island and nearby island were much lower ($\delta^{15}\text{N}$ range in ‰: [-13; 2]; Figure CA.II.2 B). This discrepancy is puzzling and further isotopic analyses are required to validate this result. On the one hand, over 60% of the range of published $\delta^{15}\text{N}$ values for terrestrial plants overlapped the one of seaweeds. This would suggest that $\delta^{15}\text{N}$ may not be reliable index for seaweed consumption based on this dataset. On the other, regarding $\delta^{15}\text{N}$ values assessed on Graham Island and nearby islands, $\delta^{15}\text{N}$ values for terrestrial plants and seaweed did not overlap. This would suggest that $\delta^{15}\text{N}$ could be used to assess seaweed consumption on the Haida Gwaii archipelago. However, when examined in the light of the range of corrected fecal $\delta^{15}\text{N}$ values, $\delta^{15}\text{N}$ values assessed for plant samples on Graham Island and nearby islands seemed extremely negative (Figure CA.II.2 C), suggesting that the negative pattern assessed for terrestrial plants may not be reliable. We thus stopped here the analysis for $\delta^{15}\text{N}$ due to the lack of confidence in our estimates of $\delta^{15}\text{N}$ values for terrestrial plants on the Haida Gwaii archipelago. This decision seemed warranted as $\delta^{15}\text{N}$ values are sensitive to environmental characteristics (see method) precluding from extrapolating $\delta^{15}\text{N}$ between different localities.

Interestingly such environmental differences might also occur between the islands of the study. Indeed, monthly $\delta^{15}\text{N}$ values assessed for Reef samples were on average $1.23 \pm 0.66\text{‰}$ and $1.28 \pm 1.14 \text{‰}$ higher than for East Limestone and Kunga samples, respectively; whereas differences in monthly $\delta^{15}\text{N}$ values between East Limestone and Kunga samples were on average $0.05 \pm 0.69\text{‰}$. The reason for such a difference between Reef, on one hand, and East Limestone and Kunga, on the other hand, could not be assessed here but may call for caution when comparing $\delta^{15}\text{N}$ values among islands in the study area.

From now, we focused our analysis on $\delta^{13}\text{C}$ values.

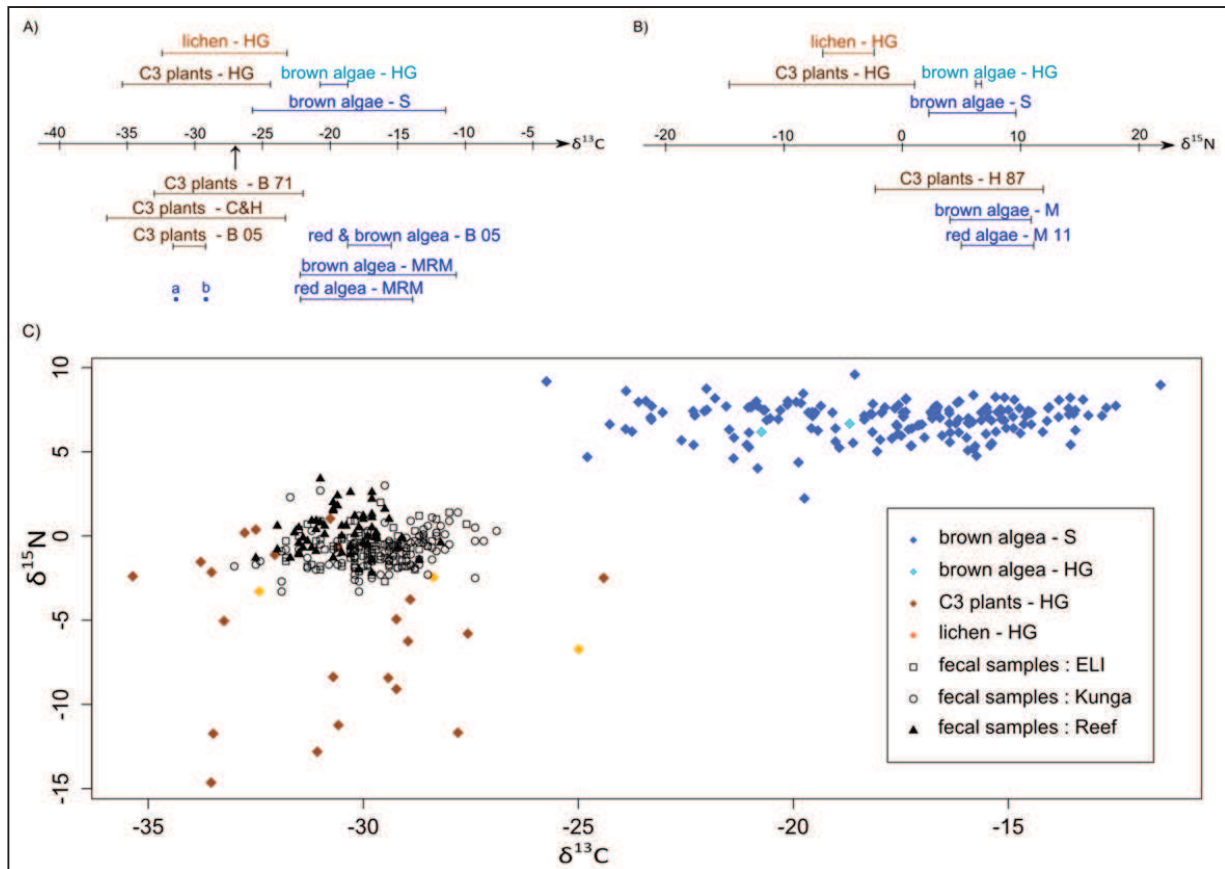


Figure CA.II.2: (A) $\delta^{13}\text{C}$ and (B) $\delta^{15}\text{N}$ ranges for terrestrial plants (brown) and seaweed (blue): Ranges below the x-axes are issued from the literature review (B 50: Balasse et al. 2005; B 71: Bender 1971; C&H 99: Cerling & Harris 1999; MRM: review from Marberly 1972, Raven et al. 2002, Marconi et al. 2011; M 11: Marconi et al. 2011). Ranges above the x-axes are issued from samples collected on Haida Gwaii (HG: plant samples collected on Graham Island and nearby islands, S: data from A. Salomon et al.). Points a, b mark extreme $\delta^{13}\text{C}$ values assessed for *Palmaria palmata* specimen collected in New Zealand and *Rhododymenia* species collected in Italy, respectively. The arrow marks -27‰, the average value for $\delta^{13}\text{C}$ in C3 plants (Bender 1971, Cerling & Harris 1999). (C) Isotopic signatures for the samples of terrestrial plants, seaweed and feces are compared according to $\delta^{13}\text{C}$ (x-axis) and $\delta^{15}\text{N}$ (y-axis) values. Isotopic values corrected for fractionation (see method) of fecal samples collected on East Limestone, Kunga and Reef are marked by open squares, open circles and closed triangles, respectively.

II.B. Correlation between isotopic values and micro-histological composition

Correlations for $\delta^{13}\text{C}$ values were globally consistent among islands (Figure CA.II.3). Negative correlations between $\delta^{13}\text{C}$ and the fecal content in monocotyledons and between $\delta^{13}\text{C}$ and the fecal content in the “other” class were observed in fecal samples from at least two islands. Positive correlations between $\delta^{13}\text{C}$ and the fecal content in dicotyledon and between $\delta^{13}\text{C}$ and the fecal content in seaweed were also detected in fecal samples from at least two islands.

However, the fecal content in seaweed was correlated with the content in other food resources. For example, the fecal content in seaweed was negatively correlated with the fecal content in monocotyledons (Figure CA.II.4 B). Considering that $\delta^{13}\text{C}$ values were also negatively correlated to monocotyledons and positively correlated with seaweeds on East Limestone and Kunga islands, the current knowledge did not allow to determine the cause of changes observed in $\delta^{13}\text{C}$ values. Increasing $\delta^{13}\text{C}$ values on East Limestone and Kunga could be due to higher consumption of seaweed and/or lower consumption of grasses (monocotyledons), with no possibility to conclude based on our current knowledge. Larger dataset would be required to identify the contribution of each food resources in $\delta^{13}\text{C}$ values. Considering that the fecal content in seaweed represented only a small fraction of deer fecal content (mean monthly content < 5%; Figure CA.II.4 A) controlled diet experiment might be required to clearly identify the contribution of seaweed in the isotopic signatures of fecal samples. This may offer interesting research perspectives.

Based on these considerations, the dataset available did not allow to use $\delta^{13}\text{C}$ values as a proxy for seaweed consumption because the correlations among fecal contents prevented from determining the origin of variations observed in $\delta^{13}\text{C}$ values, which were in addition relatively small (differences between mean monthly $\delta^{13}\text{C}$ values on East Limestone and Reed : < 1‰; < 2.5‰ on Kunga). Our analysis had thus to stop here.

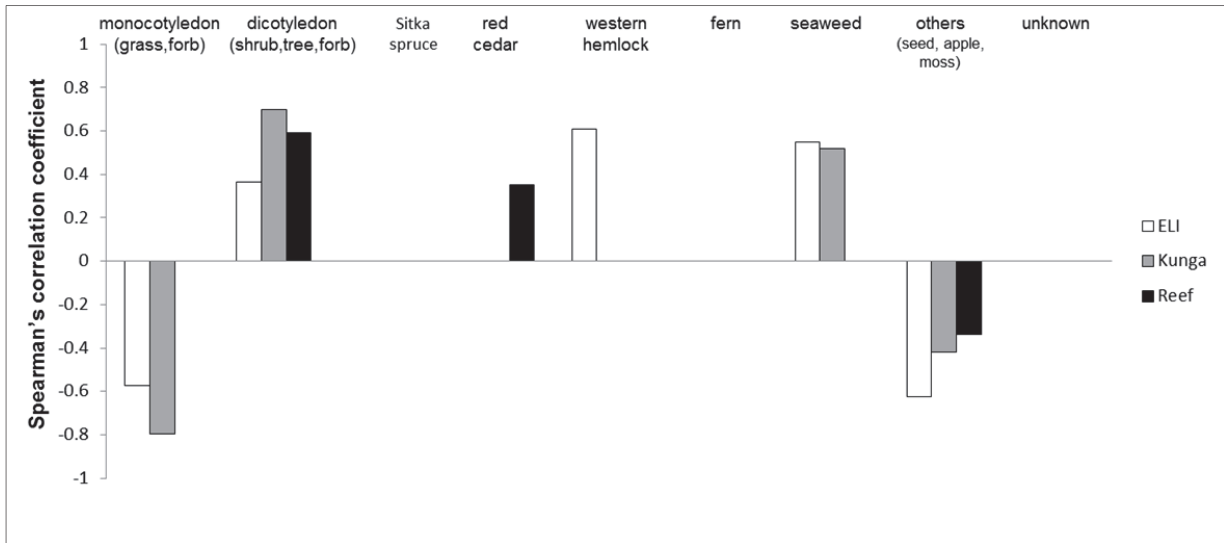


Figure CA.II.3: Spearman's correlation coefficient (Rs) calculated on the ranks of each fecal sample in relation to its micro-histological composition and its $\delta^{13}\text{C}$ value. Rs were reported only when spearman's test detected a correlation with a 10% type I error. For each micro-histological class (monocotyledon, dicotyledon, Sitka spruce, red cedar, western hemlock, fern, seaweed, other and unknown) significant Rs are presented in white for East Limestone, in grey for Kunga and in black for Reef.

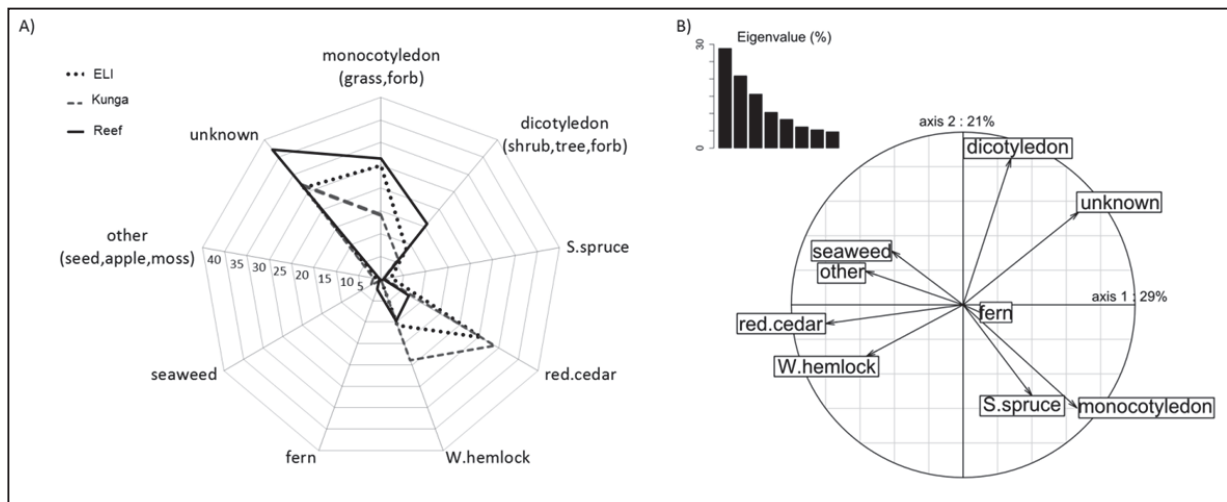


Figure CA.II.4: Fecal content of samples collected on East Limestone, Kunga and Reef in June, October 2011 and March 2012 (graph adapted from Poilvé 2013). (A) Average monthly content (%) of each micro-histological class (monocotyledon, dicotyledon, Sitka spruce (S.spruce), red cedar, western hemlock (W. hemlock), fern, seaweed, other and unknown) for the three islands (East Limestone: dotted line; Kunga: dashed line; Reef: solid line). (B) Contribution of the nine micro-histological classes for the two main axes assessed by a principal component analysis (PCA) on the micro-histological content of deer fecal sample in June, October 2011 and March 2012 (data adapted from Poilvé 2013). Eigenvalues of this PCA are presented in the top left corner.

CONCLUSION & RECOMMENDATIONS

Given the current state of our knowledge, we could not use isotopic values as a proxy to assess seaweed consumption by deer. Given the sensitivity of $\delta^{15}\text{N}$ values to environmental conditions, it is not recommended to extrapolate $\delta^{15}\text{N}$ values among localities. Plant sampling on each island is required for future analyses using $\delta^{15}\text{N}$ values. This would also help understanding why Reef fecal sample had higher $\delta^{15}\text{N}$ values systematically, a necessary step if future inter-island comparisons took place. In addition, $\delta^{15}\text{N}$ values may also vary with seasonal changes in temperature and rainfall regimes (Heaton 1987; Ambrose 1991; review in Sponheimer et al. 2003b; Codron et al. 2005b). Thus, seasonal sampling may have to be considered to validate the use of $\delta^{15}\text{N}$ values.

$\delta^{13}\text{C}$ values were more reliable for inter-locality comparison. However, low seaweed contents detected in fecal sample and the presence of confounding effects between changes in diet composition and changes in $\delta^{13}\text{C}$ values, did not allow us to use $\delta^{13}\text{C}$ values as a proxy for seaweed consumption. Low fecal seaweed contents may limit the reliability of $\delta^{13}\text{C}$ values as a proxy for the presence of seaweed in deer diet. Experimental designs controlling for deer diet may be a solution to identify the source and the relative intensity of variations observed in $\delta^{13}\text{C}$ values in relation to deer diet composition. Other isotopic signatures may also be considered, such as sulphur (e.g. Salvarina et al. 2013). Other animal samples, like hair samples, may be an interesting alternative to consider, especially if one may further explore the relationship between glucocorticoid levels and seaweed consumption since both hormone assay and isotopic analyses may be conducted in hair (e.g. Darimont & Reimchen 2002; Sponheimer et al. 2003b; Jones et al. 2006, Ashley et al. 2011). This would inform on the relationship between both components at a longer temporal scale (hair growth season). In a nutshell, isotope signature may still be promising to study the correlation between seaweed consumption and glucocorticoid levels but finer dataset are required.

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**CHAPTER III:
VIGILANCE AND INNATE THREAT-SENSITIVE FORAGING IN A
PREDATOR-NAÏVE DEER AT BAIT STATIONS**

SECTION 1:

HAVE DEER MAINTAINED TRADITIONAL VIGILANCE

AFTER 60 YEARS OF PREDATOR ABSENCE?

A STUDY UNDER CONTRASTED LEVELS OF FOOD, LIGHT AND VISIBILITY.

CHAPTER III.1: HAVE DEER MAINTAINED TRADITIONAL VIGILANCE AFTER 60 YEARS OF PREDATOR ABSENCE? A STUDY UNDER CONTRASTED LEVELS OF FOOD, LIGHT AND VISIBILITY.

“We defined two types of vigilance posture: the “overt vigilance” posture and the “general vigilance” posture: “overt vigilance” was when the animal had its head above shoulder height and was not grooming; “general vigilance” was simply when the animal had its head above ground level (either below or above shoulder height) and was not grooming”

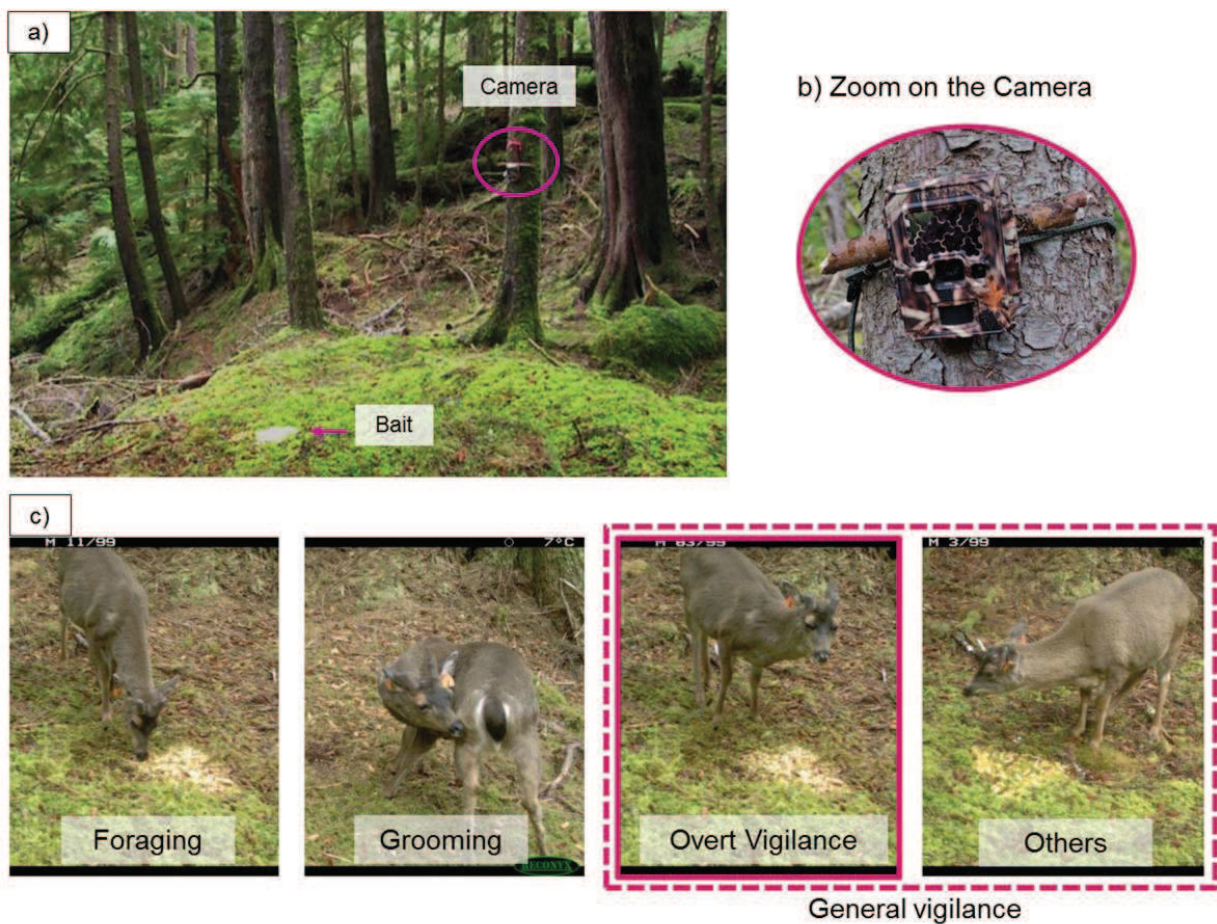


Figure C: Vigilance study at bait station. (a) shows an example of bait station set on Kunga. Bait (apples and cob) is indicated by a purple arrow. (b) zooms on the camera (J.L.Martin). (c) presents the four deer behavior identified on pictures : foraging (head at the ground level), grooming, overt vigilance (head above the shoulder) and others (head above the ground but below the shoulder and the deer is not grooming). General vigilance considered all deer postures when deer was neither foraging nor grooming.

“We estimated visibility at bait stations using a 1.5m pole with 15 alternating orange and white 10-cm stripes.”

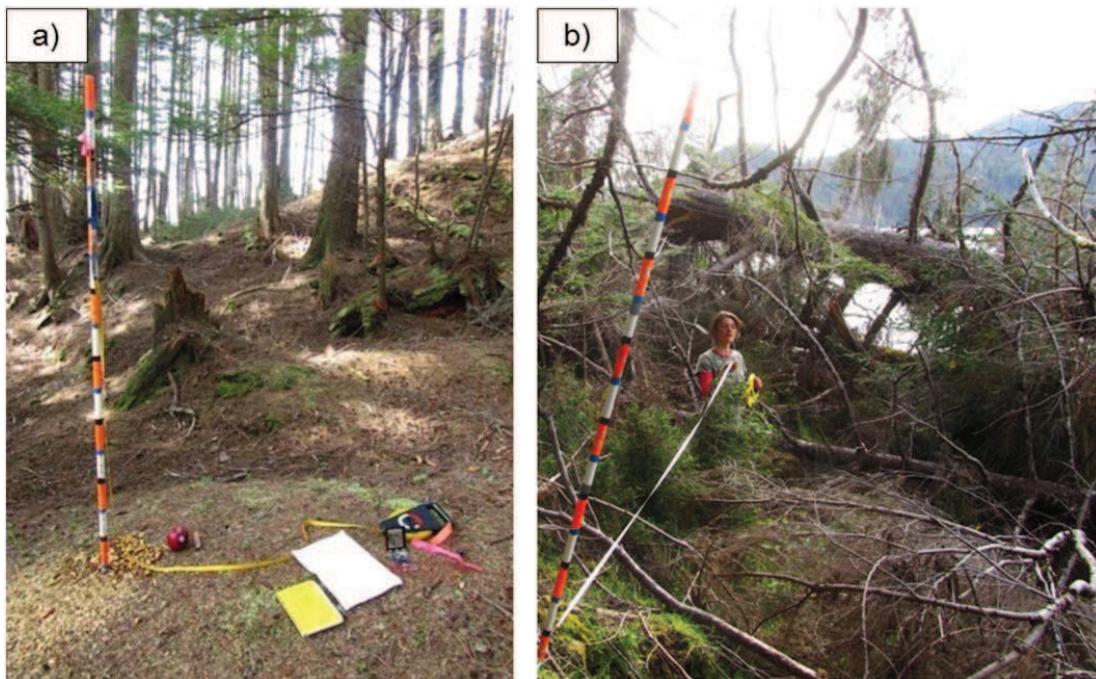


Figure D: Visibility at bait station. (a) The visibility pole is set at a bait station with a high visibility index (>50). (b) The visibility pole is set in a windfall area with a low visibility index (< 10) (S.Padié).

in preparation for Behavioral Ecology

CHAPTER III.1: HAVE DEER MAINTAINED TRADITIONAL VIGILANCE AFTER 60 YEARS OF PREDATOR ABSENCE? A STUDY UNDER CONTRASTED LEVELS OF FOOD, LIGHT AND VISIBILITY.

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KEYWORDS: apprehensive foraging, time of day, visibility, camera-trap method, predation risk, relaxed selection, risk management, trade-off, food abundance, ungulate.

ABSTRACT

Vigilance, the visual awareness of the surroundings, is a key behavior towards early detection of predators and individual survival. Time spent vigilant must be traded-off against time for other activities, particularly foraging. A reduction in risk and/or an increase in foraging needs should therefore decrease vigilance. We tested this prediction in two predator-free populations of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on Haida Gwaii. Deer colonized these islands over 60 years ago and dramatically depleted the forest plants they feed on. This provides a model situation where anti-predator vigilance has no benefits and potentially large costs. We used bait stations equipped with camera-traps to measure levels of vigilance in standardized food situations during both day and night. We expected lower vigilance levels than those observed in locations with predators and investigated how vigilance varied with (i) daylight, (ii) local visibility, and (iii) amount of bait. During the day deer spent from 9 to 18% of their foraging time in overt vigilance. This – contrary to our prediction – did not contrast much with values reported for sites with predators. Vigilance patterns differed between day and night: vigilance was lower at night, and decreased with visibility, which was not the case during the day. Vigilance differed between populations during the day but not at night. Surprisingly, bait amount had little if no effects on deer vigilance levels. Our study questions four hypotheses for the maintenance of significant levels of vigilance and their relationships with the environmental context and historical predation pressure. Our study questions the loss of anti-predation behaviors over short-time scales, and contributes to a better understanding of how animals respond to changes in levels of risk and resources.

INTRODUCTION

In response to predation prey species have developed various defense tactics, including physiological, morphological and behavioral traits (review in Caro 2005). Of these, vigilance is a key anti-predation behavior observed in most species, facilitating early detection of predators and hence reducing the likelihood of being attacked and/or caught (Lima & Dill 1990). Here we defined vigilance in its broader sense as an individual's visual awareness of its environment.

Prey generally must trade the time they devote to vigilance against other activities (e.g. foraging). It is now widely recognized that animals do not necessarily need to interrupt foraging activity to be aware of their environment and may limit vigilance costs by multitasking (e.g. scanning their environment whilst handling or chewing food: Illius & Fitzgibbon 1994; Fortin et al. 2004; Blanchard & Fritz 2007; Baker et al. 2011). Thus, low levels of vigilance can be cost-free. In addition, vigilance may not be restricted to detecting predators, and can, for example, be used in social interactions (e.g. group cohesion or intraspecific competition: Quenette 1990; Pays et al. 2010; Favreau et al. 2010). However, the levels of vigilance required to significantly reduce predation risk, because they are time-consuming, entail costs (Bednekoff & Lima 2005), and must be traded-off against the lost opportunity for foraging (Lima & Dill 1990).

Theory predicts that vigilance levels should decrease when foraging gains increase and/or when risks decrease (Lima & Dill 1990). When the marginal value of food is higher (better quality food and/or lower prey condition), the costs of lost foraging opportunities increase and prey should be less vigilant. When risks decrease, the potential fitness costs of inattention decrease, and prey should be less vigilant (McNamara & Houston 1992; Houston et al. 1993; Lima 1998; Bednekoff & Lima 1998; Lima & Bednekoff 1999; Brown & Kotler 2004). As a consequence, in situations where predation is absent, prey are expected to be much less vigilant, particularly if this leads to increased depletion of the environment (scarcity of food, poor conditions of the individuals).

This prediction has been generally supported by field studies. Most report reduced vigilance levels in areas where predator populations have been reduced or extirpated (e.g. Wolff & Horn 2003), or where prey have been introduced into predator-free environments (e.g. Blumstein &

Daniel 2005). However, food levels were rarely controlled for (e.g. Blumstein & Daniel 2002) even though prey densities generally increase in absence of predators which lead to a reduction in food abundance (e.g. Ripple & Larsen 2000) and possibly to poorer body conditions (e.g. Klein 1982; Terborgh et al. 2001). The marginal value of food is then increased which should lead to even greater decrease in vigilance (Lima & Dill 1990; Lima 1998). The respective roles of reduced risk and of increased need to forage need thus to be clarified. Additionally, vigilance was almost always surveyed during daylight (Beauchamp 2007) even though predation risk may be affected by time of day and vigilance levels may vary between day and night (e.g. Bednekoff & Ritter 1994). Considering day and night periods is thus needed to provide the full picture of individual investment in vigilance.

We addressed these limitations in a study of the possible loss of vigilance in predator-free populations of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on the Haida Gwaii archipelago (British Columbia, Canada). Deer were introduced to the archipelago 130 years ago for hunting, in absence of their main predators, wolves (*Canis lupus*) and cougars (*Felis concolor*), and with black bear (*Ursus americanus carlottae*) only present on the larger islands. Deer colonized most islands of the archipelago and reached the study islands at least 60 years ago, where they have remained isolated from predation risk (natural or hunting) ever since. On these islands browsing by deer has dramatically reduced the amount of forest understory which is the main source of deer food on the mainland (McTaggart Cowan 1956; Martin et al. 2010).

In an effort to disentangle the respective role of the absence of predation and the need to acquire food in shaping vigilance behavior, we monitored deer vigilance levels at bait stations with large or reduced amounts of bait. We did so day and night using camera-traps. Habitat characteristics (e.g. cover, visibility) are known to affect vigilance levels in presence of predation risks (Underwood 1982; Elgar 1989) but may be weakened or even lost in the absence of risks (e.g. Berger 1999; Blumstein & Daniel 2002; Wolff & Horn 2003). As the temporal scale needed for predator-free populations to lose anti-predation within a given environment is context-dependent (Coss 1999; Blumstein 2002; Lahti et al. 2009) and hence difficult to predict, we controlled for habitat openness at bait stations and investigated how vigilance of the populations studied varied with visibility.

We predicted that (1) vigilance levels should be lower than those reported for deer populations exposed to significant predation risk. Because of their past exposure to hunting during day time on Haida Gwaii or to hunting and predation by wolves (day and night) or cougars (night) on the adjacent mainland, where deer are native, it is unclear as to whether day or night were perceived as the most risky by the founders of these deer populations. We, however, predicted that (2) vigilance levels were likely to have remained higher at night when predator visual detectability is lower, especially as black-tailed deer have been shown to be more vulnerable when the probability of detecting a predator by sight is lower (Atwood et al., 2007; Lingle and Wilson, 2001; McNay and Voller, 1995). Following the same reasoning, we also predicted that (3) vigilance levels should decrease with increasing visibility, as it has been previously reported for deer in areas where predators were present (e.g. white-tailed deer (*Odocoileus virginianus*): Lagory 1986). Finally, we expected (4) deer to be less vigilant at stations with larger amounts of bait, given the high marginal value of food in a general situation of food scarcity (McNamara & Houston 1992; Beauchamp 2009).

I. MATERIAL & METHODS

I.A. STUDY AREA, HISTORY OF PREDATION AND STATUS OF THE DEER POPULATIONS

The study took place in 2011 and 2012 on two islands of Laskeek Bay on the Haida Gwaii archipelago (British Columbia, Canada): East Limestone Island (41 ha: WGS84-52.91N 131.61W) and Kunga Island (395 ha: WGS84-52.77N 131.57W).

Black-tailed deer were introduced to the archipelago between 1878 and 1925 from coastal islands off the mainland (Golumbia et al. 2008) and reached the study islands at the latest in the 1950s (Vila et al. 2004). Black bears, present on the largest islands of Haida Gwaii, are absent from the study islands. Deer from East Limestone have been reported to swim to nearby Louise Island (direct observations and unpublished GPS collar data) where black bears occur irregularly. Bears may have reached the study islands sporadically but never to stay, probably due to insufficient resources (Burlles et al. 2004). Moreover, even on the mainland, black bears are only considered as facultative and opportunistic deer predator, targeting mostly fawns (McTaggart Cowan 1956; Hatter 1982). There is no evidence that bears represent more than a very

occasional threat to deer and the studied deer are very unlikely to have experienced significant predation pressure from black bears. Deer hunting by humans is common on Haida Gwaii near populated areas and along forest roads, but has probably never occurred on the uninhabited study islands.

The absence of predation has allowed deer numbers to build up dramatically since deer colonized these islands. Deer now live at very high densities (East Limestone: possibly up to 88 deer/km², CI: [73-107], Kunga: 43 deer/km², CI: [12-144]: Chapter I), and they have dramatically impacted the understory of the closed coniferous forests of western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and Sitka spruce (*Picea sitchensis*) (Martin et al. 2010). During the winter 2010-2011, hurricane-force winds (>69 knots) occurred in our study area, creating large areas of windfall with reduced visibility.

We captured deer in March-April and late August-October 2011 under BC Wildlife Act Permit NA11-68421. We used plywood boxtraps (H:1.2m x L:2.4m x W:0.8m) securely stabilized with tight ropes. The trap has solid roof and walls and thus, when closed, the inside was in almost complete darkness and protected from rain. A small observation window could be opened when checking a triggered trap. We baited traps with 4-5 apples cut in pieces and c.500g of cob (ProForm Cob, Viterra Feed Products, Chilliwac, BC, Canada). We re-baited traps after each capture (usually once to four times a day) in order to maintain a high attractiveness of the trap. We visually checked traps which were easily accessible from base camp, at least every 6 hours during daytime and at dusk and dawn. We equipped traps located further away with VHF transmitters and monitored them remotely at least every 6 hours during the daytime and at dusk and dawn. At these traps all captures were successfully detected using the VHF signal. Traps were not activated (i.e. we removed the trigger and let the trap open) when the weather forecast suggested that we would not be able to check the traps on time. We captured and ear-tagged for individual recognition 17 deer on East Limestone (9 females, 8 males) and 18 deer on Kunga (10 females, 8 males). When checking a triggered trap we usually found deer resting or standing quietly. In each season we handled deer at the first capture only. We released deer directly without handling at all subsequent captures, which were common (>50% and >70% of deer were captured at least twice in spring and fall respectively). Handling was conducted by

opening the trap door and restraining the escaping deer in a net. The deer was immediately blindfolded. The deer was weighted in the net, which was subsequently removed and at least two people restrained the deer on its side while another recorded various information (e.g. hind foot length). Deer were ear-tagged (ear-tag dimension: 79 x 55 mm) using adapted pliers (L'Outilleur Agricole, QC, Canada). We used betadine (Purdue Pharma, US) or Aluspray (Vetoquinol, Canada) to clean the wound. Most handling (>90%) was done in less than 30 minutes. No deer showed signs of injury when released or when observed later on. During the fall season, we captured 5 lactating females which remained <8 hours in the trap. Their fawns were usually close (c.50 - 150 m) to the trap and were seen with their mothers later on. At the time of captures fawns were around 3 months old, an age at which weaning occurs (McTaggart Cowan 1956).

I.B. RECORDING BEHAVIORAL AND ENVIRONMENTAL DATA

In May-June 2011 and between late March and early May 2012 we studied vigilance of deer at 45 bait stations located either in forest (East Limestone: N = 19, Kunga: N= 16) or windfall areas (East Limestone: N = 6, Kunga: N = 4). The bait put on the ground was a mixture of c.400 g cob (ProForm Cob, Viterra Feed Products, Chilliwac, BC, Canada) and c.3 apples cut into small pieces - about 5-10 mm³ - so that deer could ingest them easily without lifting their head (Le Saout, pers. obs.). We baited stations daily to weekly to maintain a high degree of attractiveness: i.e. we re-baited when bait had been eaten or was older than a week. We changed the location of bait sites weekly to monthly to maximize the number of different individuals that might feed on the bait: i.e. a site was abandoned when no new individuals used the bait station.

We used camera-traps (Reconyx PC900) to study deer behavior at the stations with no human observers present. Cameras-traps were set up to take 1 picture per second over a period of 99 seconds each time an animal movement triggered the motion detector. The camera-traps had a built-in infrared (IR) flash with no red glow allowing pictures to be taken at night.

We validated the use of the camera-traps to study deer vigilance using tame roe deer (*Capreolus capreolus*) and demonstrated that the patterns of vigilance obtained by analyzing

picture sequences obtained from camera-traps were highly correlated to those obtained using the more common approach of analyzing video-tapes (see Supplementary Material). Note also that the validation study suggested that deer could not see the IR flash, or at least were not distracted by it (Supplementary Material).

We estimated visibility at bait stations using a 1.5m pole with 15 alternating orange and white 10-cm stripes. Visibility was estimated by temporarily placing the pole at the bait location and summing the number of stripes seen from 10 m distance in the four cardinal directions. This resulted in a numerical index ranging from 0 to 60, with a value of 60 indicating maximum visibility.

I.C. SELECTION AND ANALYSES OF BEHAVIORAL SEQUENCES

For all sequences, we recorded date, time of day and deer identity (if known from ear-tags or natural marks). We calculated the time the focal deer spent within reach of the bait. We recorded the amount of bait available at the beginning of each sequence using three classes: high, when more than 50% of the initial bait was still present and easily identifiable in a pile; low, when less than 50% of the initial bait was present, but the bait was still easily identifiable, spread on the ground with both bare and bait-covered ground; very low, when the bait was barely visible, and only present as scattered remnants. We also identified possible perturbations that occurred during the sequence, such as the presence of other deer or animals (e.g. rats, raven) that may have interacted with the focal deer.

We chose to focus on a sub-sample of all the recorded sequences, selected to provide a relevant test of our predictions (see Introduction), while limiting resampling of individuals. Our criteria were the following: (i) the visit had to have occurred during day light (between 10 min after/before civil sunrise/sunset respectively) or at night (between 110 min after/before civil sunset/sunrise respectively), but not at dawn or dusk; (ii) bait quantity had to be in the “high” or “very-low” category; (iii) deer had to have stayed at least two minutes within reach of the bait in order to calculate a reliable estimation of the level of vigilance when feeding was possible; (iv) we excluded all sequences in which interactions with other deer or animals had occurred during

these two minutes; (v) for each treatment (i.e. bait amount and day/night period), we retained only the first visit of an individually identified deer that matched the above criteria and that occurred either in forest or in windfall habitat. The habitat (i.e. forest or windfall) was not considered as a variable *per se* but enabled to maximize the range of visibility studied. This resulted in 89 sequences being analyzed (all by the same person, SLS), for a total of 16 individuals on East Limestone and 15 on Kunga.

We defined two types of vigilance posture: the “overt vigilance” posture and the “general vigilance” posture: “overt vigilance” was when the animal had its head above shoulder height and was not grooming; “general vigilance” was simply when the animal had its head above ground level (either below or above shoulder height) and was not grooming. Overt vigilance is the most common definition of vigilance in the literature (e.g. Lagory 1986; Hunter & Skinner 1998; Fortin et al. 2004; Blanchard & Fritz 2007; Pays et al. 2010) and was therefore the most useful for comparison purposes. General vigilance included all postures that could be associated with the decision to devote time to activities other than foraging or grooming. Indeed, as deer can chew and swallow food with their head at ground level, the act of raising its head can be considered as a decision *per se* of the focal animal and therefore interpreted as a potential willingness to better assess the environment, and potentially to become vigilant. Animals may be aware of their environment even while foraging, however it is recognized that lifting the head enables a better assessment of predation risk (Bednekoff & Lima 2005). Thus, we considered that our measure of general vigilance estimated the time an animal decided to devote to the assessment of its environment, including the overt vigilance posture which may be a more costly, but also more efficient, posture to assess potential risk.

For each sequence, we calculated and analyzed the proportion of time spent in overt and general vigilance postures over the first 2 minutes spent within reach of the bait.

I.D. STATISTICAL ANALYSES

To analyze how the proportion of time spent in overt and general vigilance postures varied in relation to environmental characteristics (i.e. day/night period, visibility and amount of bait), we

fitted generalized linear mixed models with a beta distribution for errors, including period of day (day vs. night), visibility (0-60), amount of bait (high vs. very low), island (East Limestone vs. Kunga) and all interactions as fixed effects (i.e. full model). Individual identity was included as a random effect on the intercept to account for the occurrence of repeated observations of individual deer in the data set. In 31 cases, the proportion of time spent in overt and general vigilance was exactly 0, which is not compatible with beta-distribution models. Thus, in all analyses, we added 0.001 to the response variable. We first tested the effect of each interaction by comparing the full model with a reduced model excluding the interaction considered. Interactions were removed when not significant. Then, the main effects of those variables that were not included in an interaction term in the model were tested by comparing the simplified model (including significant interactions only) with the reduced nested model excluding the variable considered. We identified significant effects using likelihood-ratio-tests ($\alpha = 0.05$). When a qualitative variable was identified as contributing significantly to the model's explanatory power through either a main effect or an interaction, we conducted post-hoc Tukey comparisons to investigate all pairwise differences in level of vigilance between the modalities of that variable or interaction. All analyses were conducted with R software (R Core Team 2012) and the glmmADMB and multcomp packages (Fournier et al. 2012; Bolker et al. 2012; Hothorn et al. 2013).

II. RESULTS

The proportion of time spent in overt and general vigilance varied between islands during the day, but not at night (Table III.1.1, 2). During the day deer feeding at bait stations were more vigilant on East Limestone than on Kunga (Figure III.1.1 A1; proportion of time spent in overt vigilance: Tukey: $P < 0.001$, East Limestone: c.18%, Kunga: c.9%; Figure III.1.1 A2; proportion of time spent in general vigilance: Tukey: $P = 0.010$, East Limestone: c.25%, Kunga: c.15%). However, during the night, deer were equally vigilant on both islands (Figure III.1.1 A1; overt vigilance: Tukey: $P > 0.999$, East Limestone: c.3%; Kunga: c.2%; Figure III.1.1 A2; general vigilance: Tukey: $P = 0.989$; East Limestone: c.11%, Kunga: c.9%).

The proportion of time spent in overt vigilance varied slightly with visibility, in interaction with the day/night period and the amount of bait (Table III.1.1). During the night or in presence of a high amount of bait the proportion of time spent in overt vigilance decreased by c.6% over the range of visibility considered. Over the same range it increased by c.3% during the day and by 0.5% when the amount of bait was low (Figure III.1.1 B1, C).

Table III.1.1: Statistics of the models testing the effects of the explanatory variables (day/night period, visibility, amount of bait, island) and their interactions on the proportion of time spent in overt vigilance. An effect was tested using a likelihood-ratio test comparing a reference model (which included the effect studied) with a focus model (which did not include the effect). See text for details. Log-likelihoods of the models, deviance of the focus model, and P-values are presented. Significant effects are in bold.

Tested explanatory variable	Reference model: model with the 4 main variables and	Loglik reference model	Loglik focus model	Deviance	P
Day/night period x Visibility x Bait amount x Island	4-,3-,2- way interactions	182.47	182.37	0.112	0.738
Day/night period x Visibility x Bait amount			182.35	0.036	0.850
Day/night period x Visibility x Island	3-, 2-way interactions	182.37	182.37	0.010	0.920
Day/night period x Bait amount x Island			182.35	0.044	0.834
Visibility x Bait amount x Island			182.35	0.036	0.850
Day/night period x Visibility			179.66	5.252	0.022
Day/night period x Bait amount			181.09	2.380	0.123
Day/night period x Island	2-way interactions	182.28	178.12	8.320	0.004
Visibility x Bait amount			179.58	5.406	0.020
Visibility x Island			182.02	0.530	0.467
Bait amount x Island			182.15	0.254	0.614

The proportion of time spent in general vigilance also varied with visibility in interaction with the day/night period (Table III.1.2), but was not influenced by the amount of bait (Table III.1.2). Over the range of visibility considered, the proportion of time spent in general vigilance decreased by c.13% during the night and increased by c.3% during the daytime (Figure III.1.1 B2).

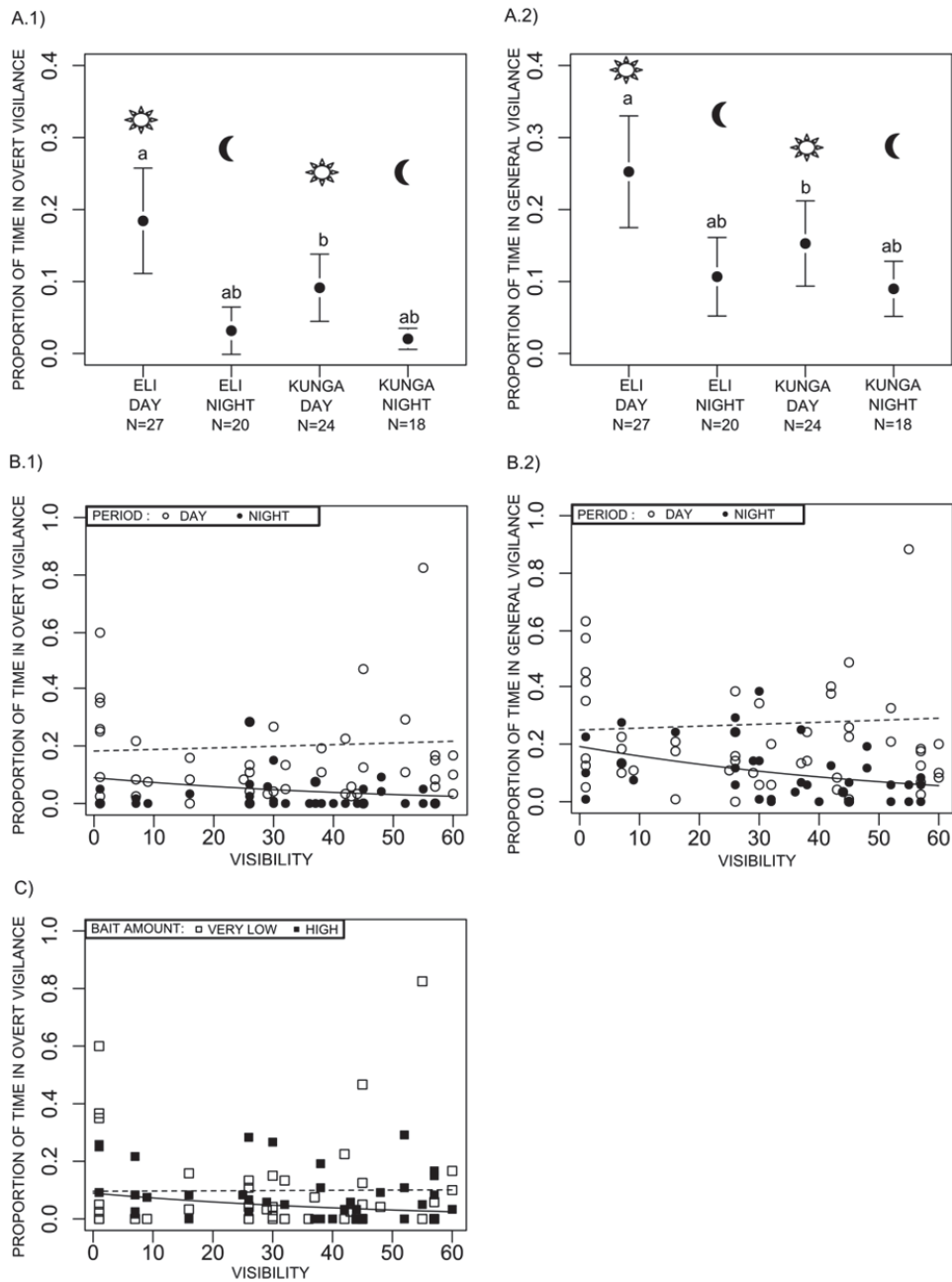


Figure III.1.1: Relationships between the proportion of time spent in overt (1) or general (2) vigilance and the interaction day/night period x island (A), day/night period x visibility (B) and visibility x bait amount (C). Vigilance was studied during the day (sun symbols, open circles and dashed regression lines) or at night (moon symbols, closed circles and solid regression lines) (Fig. A.1, A.2, B.1, B.2), and with very low (open squares and dashed regression lines) or high (closed squares and solid regression lines) amount of bait (Fig. C.1). Means and associated confidence intervals are showed for the interaction day/night period x island on deer overt (A.1) and general vigilance (A.2).

Table III.1.2: Statistics of the models testing the effects of the explanatory variables (day/night period, visibility, amount of bait, island) and their interactions on the proportion of time spent in general vigilance. An effect was tested using a likelihood-ratio test comparing a reference model (which included the effect studied) with a focus model (which did not include the effect). See text for details. Log-likelihoods of the models, deviance of the focus model, and P-values are presented. Significant effects are in bold.

Tested explanatory variable	Reference model: model with the 4 main variables and	Loglik reference model	Loglik focus model	Deviance	P
Day/night period x Visibility x Bait amount x Island	4-,3-,2-way interactions	96.136	96.056	0.161	0.688
Day/night period x Visibility x Bait amount			96.037	0.038	0.845
Day/night period x Visibility x Island	3-, 2-way interactions	96.056	96.046	0.019	0.891
Day/night period x Bait amount x Island			94.433	3.245	0.072
Visibility x Bait amount x Island			96.009	0.094	0.760
Day/night period x Visibility			90.915	6.653	0.010
Day/night period x Bait amount			93.592	1.299	0.254
Day/night period x Island	2-way interactions	94.242	91.415	5.653	0.017
Visibility x Bait amount			90.741	1.220	0.269
Visibility x Island			94.220	0.0432	0.835
Bait amount x Island			94.209	0.065	0.799
Bait amount	significant 2-way interactions	93.190	93.154	0.071	0.791

III. DISCUSSION

In this study, we used an innovative approach to study vigilance of black-tailed deer on two food-depleted and predator-free islands. Surprisingly, deer allocated a significant amount of time to vigilance during the day. Vigilance levels were broadly similar to those observed in studies where resources were less limiting and predators present. Also unexpected was the fact that the amount of bait had a very limited effect on vigilance. In addition, deer investment in vigilance showed a remarkable contrast between night and daytime in relation to the local visibility and the island.

Thus, contrary to expectations, the overall proportion of time allocated to vigilance behavior was relatively high in these deer populations which have lived without predators for over 60 years and are, in addition, facing severe depletion of their main food resources. Deer were, on average, overtly vigilant 14 +/- 16% of the time during daytime foraging bouts, which falls within the 10-20% range for levels of overt vigilance recorded in white-tailed deer on Ossabaw Island (Georgia, USA) where wolves and cougars occur (Lagory 1986). This is also within the lower range of the values recorded for overt vigilance in other deer populations exposed to carnivores and/or hunters in temperate environments, such as moose (*Alces alces*) in Denali National Park, Alaska (Molvar & Bowyer 1994: c.10-20%), mule deer (*Odocoileus hemionus hemionus*) in Northwester Utah, USA (Altendorf et al. 2001: c.16-40% in juniper forest), roe deer (*Capreolus capreolus*) in the Aurignac district, France (Benhaiem et al. 2008: c.25-35%) or Sika deer (*Cervus nippon*) in Pengze County, China (Ping et al. 2011: c.20-30%) (but see also for deer: Berger & Cunningham 1988; Laundré et al. 2001; Kloppers et al. 2005; Lung & Childress 2007; and for other ungulates : Underwood 1982; Bednekoff & Ritter 1994; Crosmarj et al. 2012; with values c.10-60%). We considered 4 non-exclusive hypotheses to explain this result:

Hyp. 1: Interference with other motivations for vigilance – As we defined overt and general vigilance as any posture adopted by a deer when it was neither foraging nor grooming, the relatively high levels of vigilance we observed may include postures linked to other behaviors such as searching for food and/or observing conspecifics (Quenette 1990; Blanchard et al. 2008). However, in our experimental set-up, centered on bait stations, food resources were locally clumped and the need to search for food was likely minimal. Indeed, in over 68% of the visits it took less than 15 seconds between deer arrival and first food intake at the bait station, suggesting that the time needed by deer to find the bait is short. Moreover the amount of bait had little to no effect on vigilance levels (see below) suggesting that food search was not the main motivation for vigilance. In addition, as we only analyzed behavioral sequences involving solitary deer, our results are unlikely to substantially reflect responses to inter-specific or social interactions, although we cannot completely exclude that, in rare instances, the focal deer may have interacted with conspecifics which were outside of the camera's field-of-view.

Hyp. 2: The shadow of rare or non-existing threats – As black bears occur on the neighboring islands, one can hypothesize that their presence may explain part of the observed levels of vigilance. However, deer on the two study islands were unlikely to have experienced encounters with black-bears and an experimental exposure of deer to bear urine on East Limestone had no effect on deer foraging behavior (likelihood of eating bait, proportion of time devoted to vigilance or time spent at bait stations) (see Chapter III, section 2). This strongly suggests that a remote chance of black bear encounter is unlikely to explain the observed levels of vigilance.

Hyp. 3: The effect of human disturbance - Human disturbance, even when not associated with actual risk, can increase vigilance in some animals (Frid & Dill 2002). Setting up and monitoring the experiments for this work necessarily involved human presence on the study islands, and thus could have influenced overall levels of vigilance observed in the animals tested. The fact that, during the day, deer were more vigilant on East Limestone, which served as base camp and also hosts crew of volunteers every spring, than on Kunga may relate to an effect of human presence. However this does not explain the overall high levels of daytime vigilance also observed on Kunga, an island where human presence is rare.

Hyp. 4: The ghost of past threats - Vigilance is a critical anti-predation behavior that may determine the outcome of a predator-prey encounter (reviewed in Caro 2005). For instance, mule deer are known to increase their chances of survival during an encounter with coyotes if they are able to detect the predator early (Lingle & Wilson 2001). Vigilance behavior should thus be under strong selection pressure (Blumstein 2002; Blumstein, Daniel & Springett 2004), and hence expected to persist over the long-term, even under relaxed selection, at least if costs in maintaining the behavior are low. Vigilance can indeed be maintained at no cost when associated with processing food (Illius & Fitzgibbon 1994; Fortin et al. 2004). Given that overtly vigilant deer were observed to be simultaneously chewing, on average 58% of the time, and assuming an underestimation of around 10% in our measure of chewing from camera-trap pictures (see Supplementary Material), overtly vigilant deer apparently spent, on average, around 70% of their time chewing. From this, a deer that spent 14% of its foraging bouts overtly vigilant (as observed, on average, in the studied populations) would actually loose only about 5% of its time in costly vigilance, supporting the idea that vigilance is often less costly than

expected (Illius & Fitzgibbon 1994; Fortin et al. 2004; Blanchard & Fritz 2007). Vigilance may therefore persist in this predator-free environment because the associated costs are too low to generate strong selection pressure for non-vigilant phenotypes within only c.20 generations. In addition, experiments conducted on East Limestone (see Chapter III, section 2) indicated that deer avoided feeding at bait stations tainted with wolf urine, despite having no experience of wolf for over 100 years. This further supports the assertion that anti-predation behaviors can be retained if they bear no costs (e.g. when the absence of the predator cues prevents the behavior to be expressed).

If vigilance bears little costs and can therefore persist over many generations then the influence of environmental drivers on vigilance should also persist. Our study indeed revealed that despite the lack of any association for several generations between visibility and actual risk, deer still responded to indirect cues of risk, such as daylight and visibility, by dedicating more time to vigilance when visibility was reduced at night. In particular, for a decrease in visibility over the range recorded, the additional proportion of time a deer devoted to overt vigilance at night was half (c.6%) the change detected in the proportion of time devoted to general vigilance (c.13%), supposedly the less costly scanning posture (Bednekoff & Lima 2005). Deer response to the indirect increase in risk with lower visibility has thus persisted.

We found that decreasing visibility had little to no effect during the daytime. This result may suggest that only very low light levels impair deer visual abilities (D'Angelo et al. 2008) and changes in visibility during the day may be less a concern for deer due to their high visual acuity in daylight (D'Angelo et al., 2008; Geist, 1981). However, a relation between vigilance and visibility is commonly found during the day in other ungulate species (e.g. Underwood 1982; Lagory 1986; Ruckstuhl & Neuhaus 2009). This may suggest that this relationship has disappeared over time in our situation. But why daytime vigilance would remain high while its relationship with visibility is lost remains an open question. A first step to address this issue would be to assess by a similar experimental design the existence of a relationship between daytime vigilance and visibility in predator-exposed black-tailed deer populations.

Finally we note that animals trade-off food for safety not only by adjusting vigilance but also by adjusting the time spent foraging in food patches (Brown 1999). Thus the changes in vigilance observed in predator-free environments may vary with the initial strategy used by the individuals. To the best of our knowledge this is an unexplored topic, both theoretically and empirically (but see Mitchell 2009). We have evidence that black-tailed deer manage risk by modulating the time spent at food patches. On East Limestone deer were not more vigilant, but stayed less time, at bait stations tainted with wolf urine (see Chapter III, section 2). In the current study deer presence was on average 25% shorter in the presence of a small rather than a large amount of bait. However, we lacked any reference data from predator-present environments to conduct meaningful comparisons. We believe studies focusing simultaneously on vigilance and time spent at food patches are required to fully understand the evolution of anti-predation behaviors.

In conclusion, our results illustrate that deer facing strong foraging constraints and living in an environment free of predators since 20 generations have retained levels of vigilance similar to the lower end of those observed in large herbivore populations exposed to predation. We also provided rare data on vigilance at night demonstrating that care should be taken when generalizing vigilance patterns observed during the day. Finally our study shows how semi-experimental studies conducted in situ could shed light on the behavioral response of prey to changes in predation risk over ecological and evolutionary time-scales.

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SUPPLEMENTARY MATERIAL III.1. CAMERA TRAPS AS A TOOL TO STUDY VIGILANCE – VALIDATION OF THE APPROACH

I. MATERIAL & METHODS

We used camera-traps (Reconyx PC900) at bait stations to study deer vigilance in the absence of human observers. We set up camera-traps programmed to acquire 1 picture per second during 99 second each time a movement triggered the motion detector. Nocturnal behaviors were recorded as well thanks to a built-in infrared (IR) flash with no red glow. We studied how estimates of vigilance behaviors obtained using this approach matched those estimated using video recording, and also investigated the effect of the IR flash on deer behavior at night.

We experimented with adult roe deer (*Capreolus capreolus*) living in enclosures at the facilities from the Institut National de la Recherche Agricole/Laboratory Comportement et Ecologie de la Faune Sauvage, at Gardouche, France. We studied deer behavior at feeding stations baited with acorns between January and February 2011.

I.A. CAMERA-TRAP VS. VIDEO- BASED ANALYSES

We compared measures of vigilance estimated from camera-trap data (at 1 image per second) to those obtained by video recording at 25 images per second. During two days we monitored vigilance of 4 animals feeding at bait stations set-up between 10:00 and 18:00. For this we used a camera-trap and a video-camera simultaneously. The 12 behavioral sequences we recorded lasted between 1.6 and 5.3 min.

We classified deer postures as follows: foraging, when the animal had its head at ground level, smelling or feeding; grooming when the animal was licking its back or its limbs; vigilant in overt vigilance, when the animal had its head above its shoulders but was not grooming (this included chewing with the head above the shoulder height); and vigilant in general vigilance, as a less restricted definition of vigilance when deer was neither foraging nor grooming (with its head either below or above shoulder height). We classified each camera-trap picture according to these postures, and on videos recorded transition times between postures. Pictures were sometimes missing within or among series of 99 pictures (between 1 and 21 consecutive

seconds could have been missed in the behavioral sequences analyzed with an average of 4 ± 5 s missed per sequence). This occurred either due to a short delay in saving pictures on the SD card (usually 1 or 2 seconds delay within a series of 99 pictures) or due to a delay in detecting a motion once the 99th picture was taken, which usually occurred when the animal was standing still for some time. We extrapolated these missing data and assumed that behavior in the missing pictures was the same as the one on the last picture taken before the missing ones.

We compared the total duration, the number and the mean duration of the overt and general vigilance bouts obtained from the camera-trap and the video-camera. For each of these variables, we fitted a linear model with the video-based data as response variable and the camera-trap-based data as explanatory variable. We used the adjusted coefficient of determination (R^2) and the intercept and slope of the regression between video- and camera-trap-based data to assess the level of similarity between the two methods.

We also investigated the error rate in detecting chewing in both overt and general vigilance postures. We first compared the total duration of chewing between video- and camera-trap-based data in both overt and general vigilance postures. We controlled for the time spent in either vigilance postures in comparing between video- and camera-trap-based data, the relative proportion of time spent chewing while in overt or general vigilance postures. We fitted linear models using the video-based data as response variable and the camera-trap-based data as explanatory variable. We assessed error rates by computing the ratio of the difference between the video- and the camera-trap-based proportion of time spent chewing in overt (or general) vigilance posture, and the video-based proportion of time spent chewing in overt (or general) vigilance posture.

I.B. IR FLASH AND BEHAVIOR AT NIGHT

We assessed the effect of the IR flash on deer behavior by placing the bait at equal distance of two camera-traps, one activated and the other one not (Figure SM.III.1.1). We recorded 37 sequences on 3 roe deer during 8 nights (2 to 3 different nights per roe deer). We defined new

behavioral sequences each time the focal roe deer was outside of the field-of-view of the active camera-trap for more than 1 min.

We classified each picture according to the 4 postures described above and also recorded whether the animal was facing the active camera-trap, the inactive camera-trap, or none (when approximately facing the median axis).

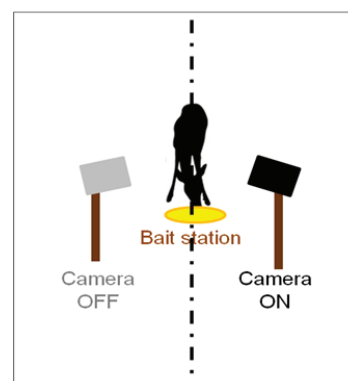


Figure SM.III.1.1: Experimental design to test the IR effect on deer nocturnal behaviour

We focused on the time spent facing either the active or inactive camera (excluding thus the time spent facing the median axis) and compared the relative proportion of time spent in either direction (i) when considering all postures and (ii) during the overt vigilance bouts only. We used a generalized linear mixed model fitted with a binomial distribution for errors with the proportion of time spent oriented towards the active camera as response variable, and with, as random factors, the sequence number nested within the night identity nested within the roe deer identity. We tested whether the proportion of time oriented towards the active camera was equal to 0.5 with a 5% risk of type I error. All analyses were conducted with the R software (R Core Team 2012) and the lme4 package (Bates et al. 2013).

II. RESULTS & DISCUSSION

II.A. CAMERA-TRAP VS. VIDEO- BASED ANALYSES

The intercepts of the linear regressions between video- and camera-trap-based data were not significantly different from 0 (Figure SM.III.1.2). The slopes of the linear regressions between video- and camera-trap based data were not significantly different from 1 (Figure SM.III.1.2), except for the mean duration of general vigilance bouts that was estimated to be 0.92 (95% CI: [0.85-0.98]). Adjusted coefficients of determination of the regressions were all estimated to be > 89 % except for the mean duration of general vigilance bouts for which R^2 was estimated to be 75% (Figure SM.III.1.2).

Overall, camera-trap-based data were very good predictors of video-based data, particularly for the total durations of each behavior. Camera-trap-based data may miss short bouts, such as brief vigilance bouts (Figure SM.III.1.2 2.b,2.c) leading to a slight overestimation of the mean duration of general vigilance bouts.

Mismatches between video- and camera-trap-based data could also arise from misclassification of behaviors which would occur when coding either dataset. To explore this hypothesis we identified mismatches in video- and camera-trap-based data and re-checked the original video- and camera-trap pictures. Often after inspection the mismatch was resolved by identifying that the behavior had been misclassified in either the video- or camera-trap-based data. This *a posteriori* evaluation revealed that observer errors accounted for 33 to 100 % of the mismatches noted between video and camera-trap data. Thus, the real accuracy of camera-trap-based assessment of vigilance patterns should be even better than suggested by the statistical models presented above, and we are thus confident that camera-traps offer a great tool for passive monitoring of animal behavior even at high temporal resolution.

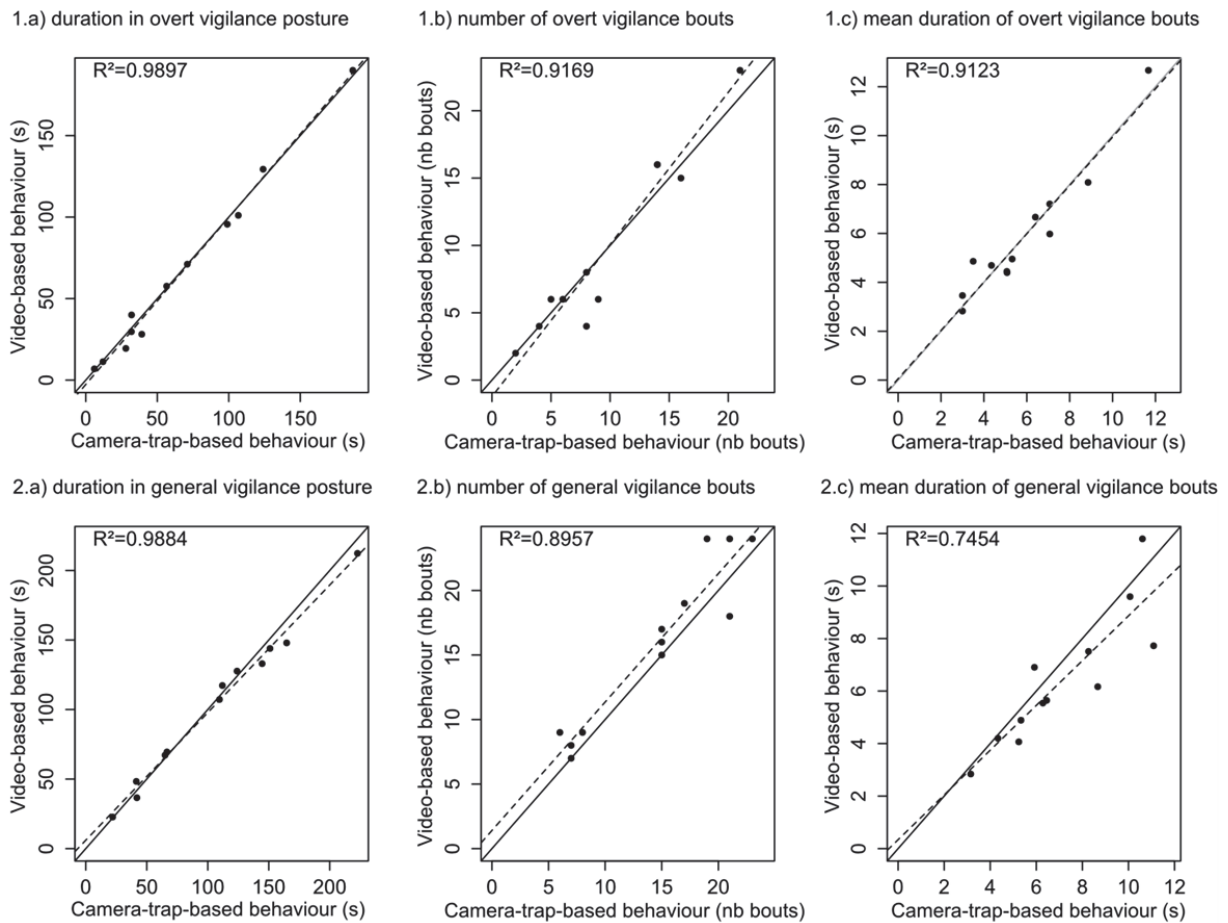
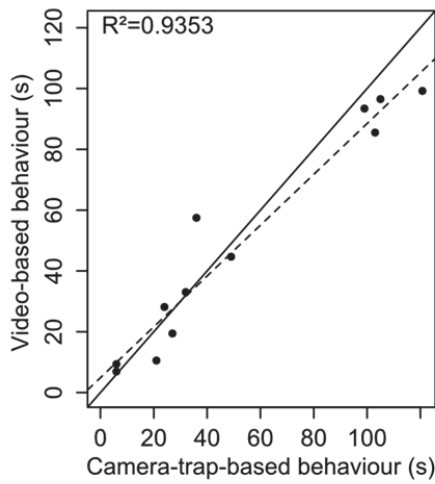
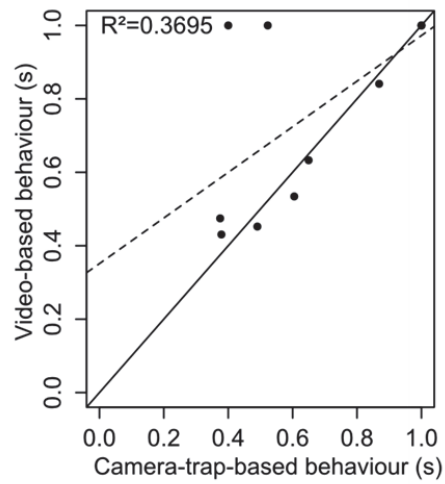


Figure SM.III.1.2: Comparison between the total duration (a), the number of bouts (b) and the mean duration of bouts (c) of overt (1) and general vigilance (2) postures between the video- (y-axis) and the camera-trap-based data (x-axis). The solid lines are 1:1 lines and the dashed line shows the linear regression of the video-based data as function of the picture-based data. Both lines overlap almost perfectly in the panel 1.a) and 1.c). Coefficients of determination of the regressions (R^2) are shown.

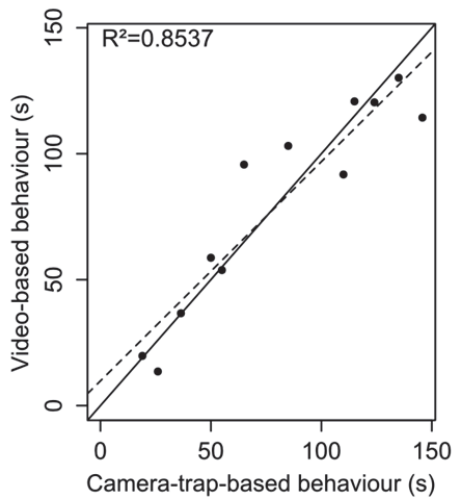
1.a) Duration of chewing bouts in overt vigilance posture



1.b) Proportion of time spent chewing in overt vigilance posture



2.a) Duration of chewing bouts in general vigilance posture



2.b) Proportion of time spent chewing in general vigilance posture

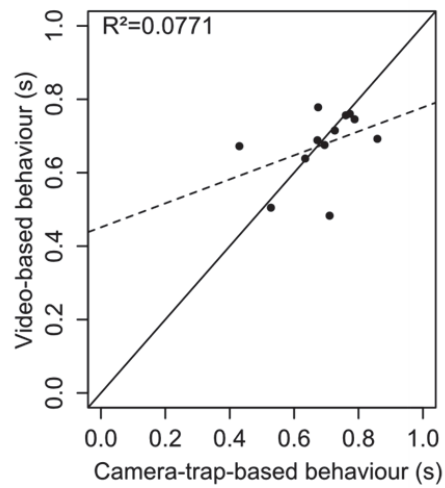


Figure SM.III.1.3: Comparison of the total duration of chewing bouts (a) and the proportion of time spent chewing (b) when deer were in overt (1) and general (2) vigilance postures between the video- (y-axis) and the picture-based data (x-axis). The solid lines are 1:1 lines and the dashed line shows the linear regression of the video-based data as function of the picture-based data. Coefficients of determination of the regressions (R^2) are shown.

The duration of chewing bouts in overt and general vigilance postures was relatively well predicted with the camera-trap-based data (Figure SM.III.1.3 1a,2a: $R^2 > 85\%$). Both omission and commission errors occurred when identifying chewing bouts. Omission errors occurred when no chewing could be identified on pictures whereas commission errors occurred when pauses in chewing were missed on pictures due to missing pictures or misinterpretation of mouth movements (e.g. licking).

These errors could be better interpreted when controlling for the duration of both vigilance postures and comparing the relative proportion of time spent chewing in overt and general vigilance postures between video- and camera-trap-based data (Figure SM.III.1.3 1b,2b). On average differences in the proportion of time spent chewing between video- and camera-trap-based data were estimated to be 9 and -3% in overt and general vigilance postures, respectively. This suggested that chewing in overt vigilance posture was more sensitive to omission error whereas chewing in general vigilance posture was equally sensitive to commission and omission errors. Indeed, for chewing in overt vigilance posture (Figure SM.III.1.3 1.b), 2 sequences (among the 12 analyzed) presented important levels of omission errors (>30% chewing time missed) but for the 10 other sequences the proportion of time spent chewing differed from video- and camera-trap-based data on average by 6% in absolute values and by 0.5% when considering compensatory effect of commission and omission errors. For chewing in general vigilance posture (Figure SM.III.1.3 2.b), 2 sequences as well presented important levels of errors (>30%), one due to commission error (47% chewing time added) and the other one due to omission error (36% chewing time missed) leading to a more balanced total error rate.

In a nutshell, camera-trap-based data may also be used to investigate finer animal behaviors (e.g. chewing). However, omission and commission errors are more likely to happen when considering subtle behaviors. In particular, chewing in overt vigilance posture is more likely to be impacted by omission error with an average error rate found to be around 9 % here.

II.B. IR FLASH AND NOCTURNAL BEHAVIOR

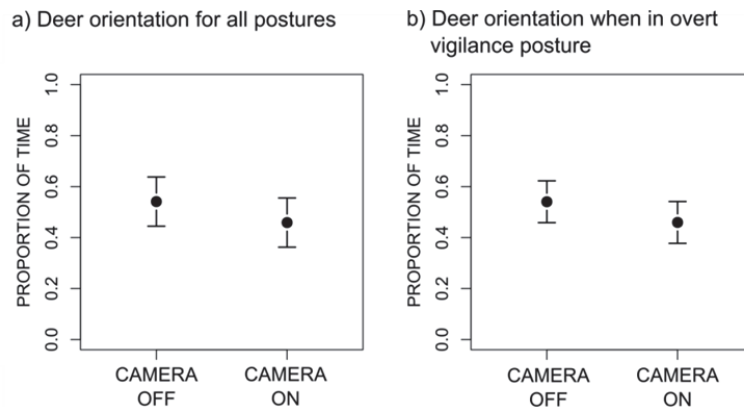


Figure SM.III.1.4: Effect of “invisible” IR flash on nocturnal deer behavior. Proportion of time spent by deer oriented towards the inactive (camera OFF) or active camera (camera ON) when considering all postures (a) and when considering only overt vigilance posture (b).

For both analyses (considering all postures or during bouts of overtly vigilance posture) deer spent similar proportions of time facing the active and the inactive cameras (including all postures: $P=0.809$, during bouts of overt vigilance posture: $P=0.809$, Figure SM.III.1.2). Deer did thus not seem to pay more attention to the active camera than to the inactive camera suggesting that they either did not see the IR flash with no red glow or were not disturbed by it.

SUMMARY

These two simple experiments enabled to test the efficiency of camera-traps as a tool to study animal behavior. We showed that discretizing animal behavior at a 1-second frequency did not impact the overall pattern of animal vigilance behavior. Frequency and mean duration of shorts events (<1 s) may be slightly underestimated and overestimated, respectively. However such ephemeral events could also be missed by observers. Thus, we considered that camera-trap may be a reliable tool to study deer behavior and may offer new opportunities to investigate nocturnal vigilance behavior as well as reducing human disturbance during wildlife observation (see O’Connell et al. (2011) for a review of possibilities offered by camera-trap).

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SECTION 2:

**INNATE THREAT-SENSITIVE FORAGING: BLACK-TAILED DEER REMAIN
MORE FEARFUL OF WOLF THAN OF THE LESS DANGEROUS BLACK BEAR
EVEN AFTER 100 YEARS OF WOLF ABSENCE.**

CHAPTER III.2: INNATE THREAT-SENSITIVE FORAGING: BLACK-TAILED DEER REMAIN MORE FEARFUL OF WOLF THAN OF THE LESS DANGEROUS BLACK BEAR EVEN AFTER 100 YEARS OF WOLF ABSENCE.

“At each bait station we sprayed 100 mL of either wolf urine, black bear urine, Cologne water, gazoline (sprayed on small cotton scent dispensers), and fresh water [...] We also filled up two eppendorf tubes”

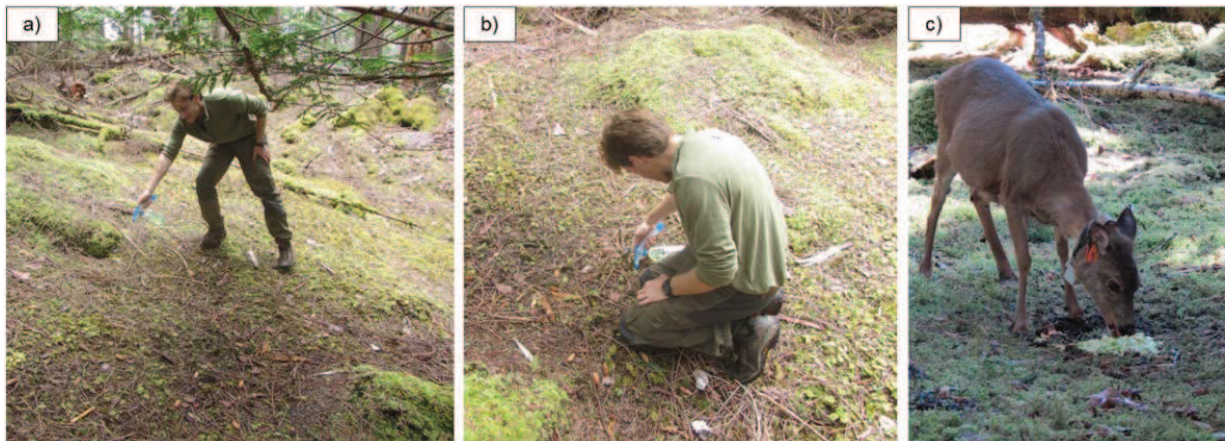


Figure E: Deer vigilance in presence of predator olfactory stimuli. (a) Olfactory stimuli (except for gazoline) were sprayed around the future bait station and (b) put into two eppendorf tubes set around the bait station. (c) Deer feeding at the bait station (S.Padié).

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CHAPTER III.2: INNATE THREAT-SENSITIVE FORAGING: BLACK-TAILED DEER REMAIN MORE FEARFUL OF WOLF THAN OF THE LESS DANGEROUS BLACK BEAR EVEN AFTER 100 YEARS OF WOLF ABSENCE.

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KEYWORDS: behavior; odor; persistence; predation risk; relaxed selection.

ABSTRACT

Anti-predator behaviors often entail foraging costs, and thus prey response to predator cues should be adjusted to the level of risk (threat-sensitive foraging). Simultaneously dangerous predators (with high hunting success) should engender the evolution of innate predator recognition and appropriate anti-predator behaviors that are effective even upon the first encounter with their predator. The above leads to the prediction that prey might respond more strongly to cues of dangerous predators that are absent, than to cues of less dangerous predators that are actually present. In an applied context this would predict immediate and stronger response of ungulates to the return of top-predators such as wolves in many parts of Europe and North America than to current, less threatening, mesopredators. We investigated the existence of innate threat-sensitive foraging in black-tailed deer. We took advantage of a quasi-experimental situation where deer had not experienced wolf predation for ca. 100 years, and were only potentially exposed to black bears. We tested the response of deer to urine of wolf (dangerous) and black bear (less dangerous). Our results support the hypothesis of innate threat-sensitive foraging with clear increased passive avoidance and olfactory investigation of cues from wolf, and surprisingly none to black bear. Prey which have previously evolved under high risk of predation by wolves may react strongly to the come-back of wolf cues in their environments thanks to innate responses retained during the period of predator absence, and this could be the source of far stronger non-consumptive effects of the predator guild than currently observed.

INTRODUCTION

Predation risk is a key driver of fitness, and accordingly animals have developed numerous anti-predator behaviors to minimize this risk (Lima and Dill 1990 ; Curio 1993; Lima 1998; Caro 2005). These behaviors often entail costs such as reduced foraging (e.g. Brown and Kotler 2004). It has therefore been hypothesized that the strength of anti-predator behavior should be adjusted to the level of risk experienced by the prey (threat-sensitive predator avoidance hypothesis: Helfman 1989).

A key determinant of the level of threat is the dangerousness – the lethality – of the predator, which may be defined as the likelihood of death for the prey after an encounter with the predator. Anti-predator behavior has been found to be sometimes related to the dangerousness of the predator, but not always. When offered a choice between refuges with odors of more or less dangerous snakes, mountain log skinks usually select the refuge treated with the odor of the less dangerous snake (Stapley 2003). On the contrary, velvet geckos show similar response levels towards odors of five species of snakes that differ widely in threat (Webb et al. 2009). Small-sized deer are found to browse less (Swihart et al. 1991; white-tailed deer) or more (Sullivan et al. 1985; mule deer) on trees treated with bobcat (more dangerous) urine than on trees treated with coyote (less dangerous) urine. Thus, although there is generally good support for a relationship between the level of threat posed by a predator and the level of responses of the potential prey to these threats (for instance Vilhunen and Hirvonen 2003; Botham et al. 2006; Blumstein et al. 2008), studies rejecting the hypothesis of such a relationship remain frequent (for instance see also Amo et al. 2004; Gonzalo et al. 2008).

The ability of individuals to recognize predators and the risk they represent may actually depend on the ontogeny of this recognition. Failures of prey to recognize and respond appropriately to dangerous predators with high rates of attack success, act as forces of selection for the evolution of innate (i.e. not learned) responses (Mery and Burns 2010). Individual learning should be counter-selected, whereas social learning could improve predator recognition and allow finer adjustments of the response to the level of threat (Kelley et al. 2003; Griffin 2004; Brown et al. 2011). The strength of selection for innate or learned responses could differ with

the type of cues. It has been suggested that innate recognition of, and response to risk may be more common for visual or auditory than for olfactory (i.e. chemical) cues, as visual and auditory cues are likely associated with a more immediate risk to which an absence of response may be more risky (e.g. Blumstein 2002). However, predator odors have actually often been shown to elicit innate anti-predator response (e.g. Apfelbach et al. 2005; see also Kobayakawa et al. 2007).

How long innate anti-predator responses to the more dangerous predators will persist in the absence of those predators remains uncertain however. This will likely depend on the costs of anti-predator responses, mutation rates and possible pleiotropic effects (Coss 1999). The persistence of innate anti-predator responses triggered by odors of naturally dangerous predators has been demonstrated many times using laboratory rodents which have not experienced predation for hundreds of generations (Apfelbach et al. 2005; Fendt et al. 2006). In the wild the presence of less dangerous predators might also facilitate the persistence of responses to more dangerous predators that are absent if cues are similar or recognition processes genetically linked (Blumstein 2006; Blumstein et al. 2006). There are therefore many reasons to believe that innate threat-sensitive foraging, if present, would have persisted in species with a relatively long generation time in areas where dangerous predators have been historically removed or displaced by human activities. Confirming this may be crucial in the context of wolves returning to many parts of Europe and North America (Boitani 2003). For the ca. 100 years wolves have been absent, their prey have been exposed only to less dangerous predators such as black bears, coyotes or foxes, species that are better tolerated by humans. How will such prey react to returning wolves, how does this response compare to their reaction to cues associated to the less threatening predators that had remained present, and will thus lead to increased non-consumptive effects imposed on prey?

As a first step towards answering these questions we took advantage of a quasi-experimental situation. We investigated if black-tailed deer (*Odocoileus hemionus sitkensis*) introduced 100 years ago on the archipelago of Haida Gwaii (British Columbia, Canada), an area devoid of wolves but with black bears potentially present, showed innate threat-sensitive foraging with respect to these two predators. We used bait stations to study the response of deer to a set of

olfactory cues including urine of wolf (dangerous) and black bear (less dangerous). Animals can reduce risk by either being more vigilant or spending less time in risky areas (Brown & Kotler 2004), so we measured these two variables to provide a comprehensive study of deer behavioral response. We predicted that deer would display increased apprehension (being more vigilant and/or staying less time) at bait stations scented with bear urine than with control or foreign odors, and even higher apprehension at bait stations scented with wolf urine.

I. MATERIAL & METHODS

I.A. STUDY SITE

Our study took place on East Limestone (52°54'27N, 131°36'48W), on the Haida Gwaii archipelago off the West coast of Canada. Black-tailed deer were introduced on the archipelago in 1878 and 1911-1925 from coastal islands near Prince Rupert on the mainland, and had reached East Limestone by the 1950s (Golumbia et al. 2008). Wolves (*Canis lupus*) are absent from the archipelago, but are widely dispersed throughout the deer range on the mainland and on coastal islands, where they are one of the main deer predators (Darimont et al. 2004). Although wolves have generally moderate hunting success on small-sized deer, they still represent a significant threat to adult (and young) deer (Mech and Peterson 2003). The black bears present on the archipelago belong to the largest sub-species (*Ursus americanus carlottae*). Black bear predation on black-tailed deer occurs mostly on fawns, although there is anecdotal evidence that adult deer are sometimes chased with little success (Zager and Beecham 2006). Black bears are not continuously present on East Limestone, but are common on the larger neighboring Louise Island. Deer frequently commute between the two islands (unpublished data from direct observations and GPS collars) and thus at least some East Limestone deer are likely to have encountered bear cues. Note also that at the time of the study most females had dependent juveniles, as birth occurs in May/June. Hunting by humans has always been sporadic and did not occur on East Limestone for at least 25 years. The deer population density exceeds 30 individuals per km². Deer have severely over-browsed their environment leading to a dramatically simplified ecosystem and poor resource availability compared to the initial environment (Martin et al. 2010).

I.B. FIELD EXPERIMENT AND STATISTICAL ANALYSES

We used bait stations to study the response of black-tailed deer to the odor of wolf and bear urine, which were compared to their response to one control odor (water) and two novel odors (gazoline, Cologne water). During the course of July 2012 we set-up 98 baits stations whose locations were randomly selected, with the constraint to be on flat ground and in open understory. Two stations baited within a 5-day window were always separated by at least 50 m. Due to the small size of the island and in order to maximize the distance between non-water treatments, 23 locations were used twice. In these cases the initial treatment applied was always water. A deer could visit several stations in a day (see discussion below on resampling). This design, imposed by the small size of the island, is conservative. Indeed, if deer behavior at a station depends on previous experience at bait stations, this would tend to mask differences between treatments, rather than exacerbate them.

At each bait station we sprayed 100 mL of either wolf urine, black bear urine, Cologne water, gazoline (sprayed on small cotton scent dispensers), and fresh water from an island stream, this over a circle of approximately 1 m in diameter. We also filled up two eppendorf tubes which were kept open and pushed into the ground in the same area, allowing us to check visually the persistence of a source of odor. We then dropped two apples, cut into pieces, at the center of the circle. The apples were always dropped after spraying the odor, and were thus not stained. We had purchased urines at Murray's Lure (www.murrayslures.com). They were collected from captive animals via floor collection drains in pens, and kept in airtight containers in a cool dark cellar. The observed response to wolf odor (see Results) suggested that odors had been well preserved (see Bytheway et al. 2013 on the influence of odor age).

Deer behavior at bait station was monitored using camera-traps (Reconyx © PC900) set-up to acquire 1 picture per second during 99 second each time an animal movement triggered the motion detector (detection range: ~ 30 m). The bait station was checked approximately every 8h, and the monitoring ended once the bait had been eaten, or after approximately 24h. In all cases the eppendorf tubes were still filled up with liquid, indicating that deer foraging on the apples would have smelt the treatment odor. When several deer had visited the bait station

before the monitoring stopped, we only analyzed pictures from the first deer visiting the bait, to avoid confounding effects related to the amount of bait. Each bait station was used only once.

We analyzed the pictures taken by the camera traps and recorded (1) if the bait station had been visited; (2) the time elapsed between the setting of the bait and the first visit by deer; (1) and (2) are indicators of potential passive avoidance of the odor at a range greater than the operating range of the camera's motion detector; (3) if the deer ate the bait – this was coded as a binary yes/no variable, which was fully justified as in virtually all cases the bait was either untouched or fully eaten; (4) the proportion of time the deer was in the “sniffing” posture (head lying low, nose extended); (5) the vigilance level while eating the bait, measured as the proportion of time spent the head up while being able to reach the bait without moving; (6) the time spent at the bait station. By definition, sample size decreased from (1) to (4-5), and was also affected by occasionally missing information (bait being eaten by squirrels or ravens, issue with the camera-trap). Actual sample size for each analysis is reported in Figure III.2.1 and Figure SM.III.2.1. Pictures were analyzed by H.M. without prior knowledge of the treatments. H.M. also recorded individual identity of the deer when marked with ear-tags (deer captures and marking are routinely conducted). Marked individuals represented 41 % of the observations.

The effect of the odor treatment was studied using generalized linear models including treatment as explanatory variable (and duration of the camera deployment for the analysis of likelihood of visit). The models had either a binomial (for the analysis of likelihood of visit, likelihood of eating the bait, and percentage of time sniffing and vigilant) or negative binomial (for the analysis of time before first visit and time spent at bait station) distribution of errors. We used post-hoc Tukey comparisons to study the significance of all pairwise differences between treatments. We accounted for unequal variance between treatments by using heteroscedastic consistent covariance HC3 sandwich estimation (Herberich et al. 2010).

Marked individuals were seen on average ca. 1.7 times per treatment, suggesting that some moderate level of resampling was present in the data. Mixed models could not be used to account for this resampling, as the large proportion of unmarked individuals prevented us to

use deer identity as a random covariate. Therefore, we used a highly conservative α -level of 1 % to assess statistical significance. Note also that effect size – which is insensitive to resampling – of significant results discussed here were large (see Table III.2.1). Analyses were conducted using the R statistical software (R Core Team 2012), *multcomp* (Hothorn et al. 2008) and *sandwich* (Zeileis 2004) packages.

II. RESULTS

The likelihood that a deer visited a bait station did not differ between odor treatments other than the Cologne treatment, for which this likelihood was slightly to moderately higher than for all others treatments (Table III.2.1 a; Figure SM.III.2.1 a). The time before the first deer visit did not differ between odor treatments (Table III.2.1 b; Figure SM.III.2.1 b). When visiting a bait station deer almost never ate the bait when presented in conjunction with wolf urine odor, whereas they almost always ate baits under other treatments (Figure III.2.1 a; Table III.2.1 c). Notably, all of the 7 marked individuals who were seen at baits associated with wolf urine odor did not eat the bait whereas they always did eat baits associated with other odors. Wolf urine odor also induced much higher levels of sniffing than any other odor (Figure III.2.1 b; Table III.2.1 d). Vigilance did not increase significantly at stations associated with wolf urine odor (Figure III.2.1 c; Table III.2.1 e). Bear urine odor induced higher rate of sniffing than observed at water or cologne treatments (Figure III.2.1b; Table III.2.1 d), but did not lead to increased vigilance level (Figure III.2.1 c, Table III.2.1 e). Finally, deer spent far less time at stations treated with wolf urine, whereas time spent did not differ between bear and control treatments (Figure III.2.1 d, Table III.2.1 f).

Table III.2.1. Results from pairwise between-treatment comparisons for all response variables (columns a-f). Comparisons were conducted using Tukey simultaneous comparisons tests, accounting for unequal variance between treatments by using heteroscedastic consistent covariance HC3 sandwich estimation. The comparisons are expressed on the original scale of the response variable. Estimates and their 99 % confidence intervals (brackets) are reported. Estimates for which the 99 % confidence interval does not include 0 are in bold and where considered significant. Odor treatments were water, Cologne water, gazoline, wolf and black bear urine. There was no variability in the likelihood of deer eating the bait for the Cologne water and gazoline treatments, so estimates of between-treatment comparisons could not be computed for those. See Fig. 1a of the article for visual inspection of these data.

	a. Likelihood of deer visiting the bait station	b. Time before the first deer visit (hours)	c. Likelihood of deer eating the bait	d. Level of sniffing when deer could reach the bait (% of time)	e. Level of vigilance when deer could reach the bait (% of time)	f. Time spent at bait station (minutes)
Wolf - Bear	0.065 [-0.575 / 0.150]	2.109 [-2.863 / 18.190]	-0.790 [-0.931 / -0.019]	0.418 [0.066 / 0.820]	0.186 [-0.074 / 0.650]	-8.621 [-10.443 / -2.020]
Wolf - Cologne	-0.088 [-0.637 / -0.005]	4.259 [-1.207 / 26.980]	N/A	0.453 [0.052 / 0.919]	0.257 [-0.041 / 0.859]	-17.528 [-19.271 / -11.845]
Wolf - Gazoline	0.241 [-0.464 / 0.326]	4.132 [-2.383 / 72.790]	N/A	0.449 [0.084 / 0.867]	0.204 [-0.025 / 0.580]	-5.409 [-7.169 / 0.461]
Wolf - Water	0.105 [-0.481 / 0.189]	2.344 [-2.642 / 18.577]	-0.770 [-0.907 / -0.979]	0.454 [0.116 / 0.838]	0.218 [-0.011 / 0.595]	-9.157 [-10.895 / -3.517]
Bear - Cologne	-0.154 [-0.154 / -0.154]	2.151 [-6.473 / 4.342]	N/A	0.034 [-0.020 / 0.038]	0.071 [-0.511 / 0.129]	-8.906 [-36.260 / 2.661]
Bear - Gazoline	0.175 [-0.138 / 0.783]	2.023 [-26.182 / 4.789]	N/A	0.031 [-0.031 / 0.037]	0.018 [-0.313 / 0.111]	3.213 [-8.199 / 7.889]
Bear - Water	0.040 [-0.557 / 0.183]	0.235 [-9.689 / 3.495]	0.020 [-0.065 / 0.816]	0.036 [0.019 / 0.038]	0.033 [-0.277 / 0.114]	-0.535 [-16.279 / 6.168]
Water - Cologne	-0.194 [-0.194 / -0.194]	1.915 [-1.712 / 16.266]	N/A	-0.001 [-0.003 / 0.031]	0.038 [-0.055 / 0.643]	-8.372 [-14.144 / 3.051]
Water - Gazoline	0.135 [-0.175 / 0.733]	1.788 [-2.592 / 46.599]	N/A	-0.005 [-0.007 / 0.014]	-0.014 [-0.084 / 0.175]	3.747 [-2.252 / 16.093]
Cologne - Gazoline	0.333 [0.023 / 0.910]	-0.127 [-32.902 / 2.676]	N/A	-0.003 [-0.115 / 0.003]	-0.053 [-0.673 / 0.054]	12.119 [3.608 / 16.222]

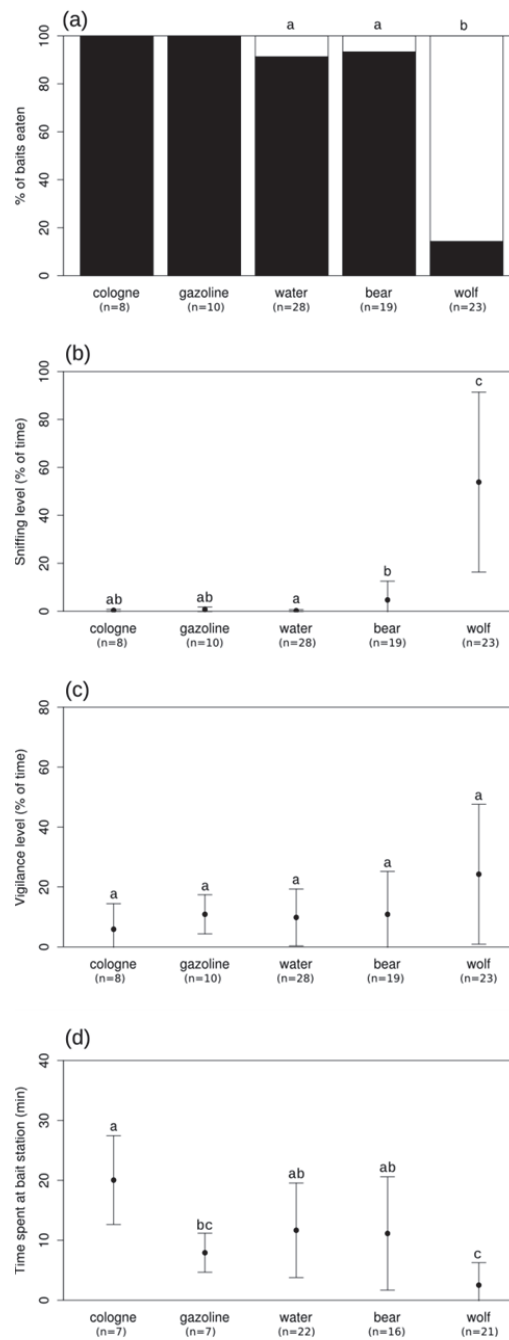


Figure III.2.1 Effect of odor treatments on (a) the percentage of baits eaten (over events of actual deer visit to bait stations); (b) the percentage of time spent in sniffing posture (i.e. head low, nose extended) and (c) vigilance posture (i.e. head-up) (over time during which the deer could reach the bait, in both (b) and (c)); (d) the time spent at the bait (in minutes). In panels (b-d) mean and standard deviations are shown, and in all panels treatments with the same lowercase letter were not significantly different (Tukey post-hoc comparison tests at $\alpha = 0.01$ significance level)

III. DISCUSSION

Our results clearly demonstrate that black-tailed deer on Haida Gwaii archipelago react more strongly to wolf cues than to cues associated with the less dangerous black bear, despite having had no contact with wolves for more than 100 years. This is in accordance with – but do not prove (see below) – the innate threat-sensitive foraging hypothesis. The greater response of deer to wolf cues than to black bear cues is indeed consistent with the difference in the lethality these predators represent for black-tailed deer. Wolves usually have moderate hunting success for small-sized deer (Mech and Peterson 2003), but are still far more efficient predators than black bears which usually predate fawns, only occasionally attacking adults and with low success (Zager and Beecham 2006). Our observation that odor from black bear urine did neither affect the likelihood of eating the bait nor the vigilance levels was somewhat unexpected. Sniffing rate was higher under black bear urine treatment than for water treatment, thus ruling out that deer could not differentiate between the two treatments. Multiple explanations could elucidate this absence of response to black bear cues. First, black-tailed deer as a species may not have evolved responses to black bear when foraging without their young, as bears are mostly a threat to juveniles. This is very unlikely as other studies have shown that other small-sized deer or even larger herbivores do respond to black bears while foraging (e.g. Cowan 1956; Berger et al. 2001). Second, the depleted environment in which the study was conducted could favor foraging over what is perceived as a limited risk, reducing expression of anti-predator behaviors (despite predator recognition) in the absence of immediate or more explicit risky situations. Physiological information such as heart rate could have clarified this but could not be collected. Third, responses to black bear may have to be learned and some deer may never have had the opportunity to learn as black bear presence is uncommon at our study site. If true this would support even more strongly the innate threat-sensitive hypothesis. A formal demonstration of this hypothesis would require replicating predator cues at similar levels of dangerousness, as done recently in a study of behavioral impacts of predator hunting modes (Miller et al. 2013). The behaviors observed at bait stations scented with wolf urine differed from those observed when scented with control or novel odors, suggesting that this was not a random response. The current study design does not allow differentiating a threat-sensitive response from a response

based on other criteria than dangerousness however, and was mostly intended to falsify the threat-sensitive foraging hypothesis. Because large mammals also usually have few predators, a study replicating cues at similar levels of dangerousness might be complex to achieve for this taxa. In our situation we could have used puma (*Felis concolor*) and coyote (*Canis latrans*) urine, which are respectively dangerous and less dangerous predators of deer in many places. However this could not be undertaken here for logistical reasons, and would not have been free of caveats, as deer introduced on Haida Gwaii did not experience coyote predation for at least several decades. Note that our results are also consistent with the alternative hypothesis that the odor of wolf urine better predicts the presence of wolves than the odor of bear urine predicts bear presence. We suggest that this is unlikely, as wolves usually range more than black bears, and thus are less likely to be found close to urination sites. The odor of bear urine is therefore more likely to be associated with the close presence of bear than the odor of wolf urine to be associated with the close presence of wolves.

Studies in other taxa have shown that innate predator recognition and associated responses may sometimes persist for hundreds to thousands of generations (e.g. Coss 1999; Stankowich and Coss 2007, Li et al. 2011; Durand et al. 2012). Innate anti-predator behavior could persist in the absence of a predator because of other sources of selection (either via the presence of other predators or via pleiotropic effects on other functional traits), because of limited genetic drift and highly reduced genetic variance caused by previously strong selection, and/or because of the low current fitness costs of the behavior (Coss 1999; Lathi et al. 2009). A combination of the latter two is likely to occur for behaviors expressed after the perception of a predator cue. Indeed, by definition the fitness cost of these behaviors is nil in the absence of a predator and thus of its cues, except for situations in which other predators produce similar cues (see discussion in Blumstein 2006; Blumstein et al. 2006). Thus, we expect that under relaxed selection innate post-stimulus (ie. after detection of a cue) anti-predator behavior will wane mostly through genetic drift, and particularly slowly as genetic variability of these strongly selected for traits is likely to be small. To the best of our knowledge one cannot for now estimate a priori the speed at which this will occur, as one would need to know mutation rates and how gene functions are affected by mutations. Thus, differences in intensity of innate anti-

predator response to different predators should also persist over long periods of time unless cognitive processes involved in predator recognition are disrupted (see discussions in Coss and Ramakrishnan 2000; Stankowich and Coss 2007).

Our study contrasts with results from Berger et al. (2001) who showed that wolf-naïve, but black bear experienced moose of southern Greater Yellowstone increased their vigilance in response to black bear olfactory cues, but had ceased to respond to wolf olfactory cues after over 80 years of wolf absence. This result is particularly surprising given that moose weight 4 to 15 times more than black-tailed deer, and are thus less vulnerable to black bear attacks. This absence of threat-sensitivity was further supported by the observation that the moose tested never abandoned sites during the experiments with either wolf or black bear cues, whereas wolf- and black bear experienced moose from Alaska abandoned sites more often when exposed to black bear than to wolf odor. While these results did neither support the threat-sensitivity hypothesis nor the persistence of anti-predator response to wolf olfactory cues, Berger et al. (2001) presented in the same study another experiment supporting the persistence of anti-predator response to wolf auditory cues, a pattern also revealed by Blumstein (2002) in macropods. Further studies will likely be required to understand such discrepancies. We note that the observers were close and visible to moose in Berger et al. (2001), whereas in our study the odor display was not associated with actual human presence. But it is uncertain to what extent this could have affected the animal reaction's to predator olfactory cues, and why it would reverse the patterns observed.

Animals can mitigate risk by using vigilance and/or time allocation (Brown and Kotler 2004), and deer used both when facing signs of wolf presence. The foraging/predation risk trade-off was dealt with by completely giving-up the feeding opportunity despite its immediate availability. Deer could have decided to feed at a slow rate while being overly vigilant (as was observed after carnivore reintroduction by Hunter and Skinner (1998) and Laundré et al. (2001)), but this was not the case, and we conclude that the perceived cost of foraging was mostly the increased time spent in a possibly risky area. In this depleted environment the giving-up of a usually attractive resource indicated the dramatic weight given to the perceived risk by the animals and the

possibly high costs of non-consumptive (i.e. trait-mediated) effects of predators on their prey (Preisser et al. 2005).

Our study contributes information supporting ecologists' recent endeavor to better understand changes in ungulate behaviors in localities where abundant ungulate populations face the return of wolves. Prey species that have previously evolved under high risk of predation by wolves may react strongly to the come-back of wolf cues in their environments thanks to innate responses retained during the period of predator absence. We have shown that these responses may dramatically affect foraging, even in depleted environments, and lead to expectations of high non-consumptive effects of predators. We also call for further studies investigating the hypothesis of threat-sensitivity predator avoidance in ungulates. At the same time as the role of mesopredators – which have often remained the only non-human source of risk for prey after wolf extirpation – is being increasingly recognized (Prugh et al. 2009), the return of apex predators will again reorganize the trophic food web in space and time and force ungulates, the main prey of these apex predators, to respond (or not) to the contrasted risks now reinstated (Ritchie et al. 2012).

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SUPPLEMENTARY MATERIAL III.2.

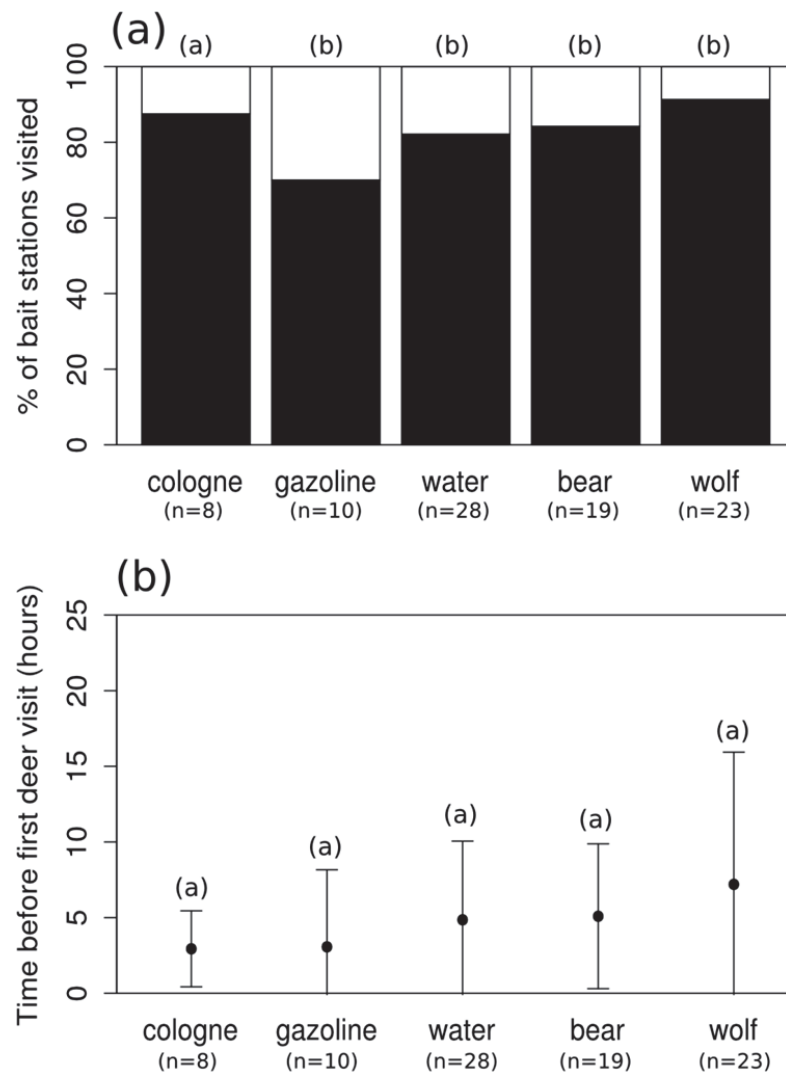


Figure SM.III.2.1: Effect of odor treatments on (a) the proportion of bait stations visited by a deer; (b) the time before the first deer visit. In panel (b) mean and standard deviations are shown, and in all panels treatments with the same lowercase letter were not significantly different (Tukey post-hoc comparison tests at $\alpha = 0.01$ significance level)

**CHAPTER IV:
MANAGING DEER-FOREST INTERACTION THROUGH FEAR:
TESTING THE SHORT TERM EFFECTS OF LOW INCIDENCE
HUNTING ON NAÏVE DEER.**

CHAPTER IV: MANAGING DEER-FOREST INTERACTION THROUGH FEAR: TESTING THE SHORT TERM EFFECTS OF LOW INCIDENCE HUNTING ON NAÏVE DEER.

“The hunt took place during daytime between May 1 and 25, 2012 on the South coast of Kunga [...] We monitored deer presence during the day on four beaches by using [...] camera traps [and] monitored growth and browsing rate of four fast-growing plant species present in the coastal forest”.

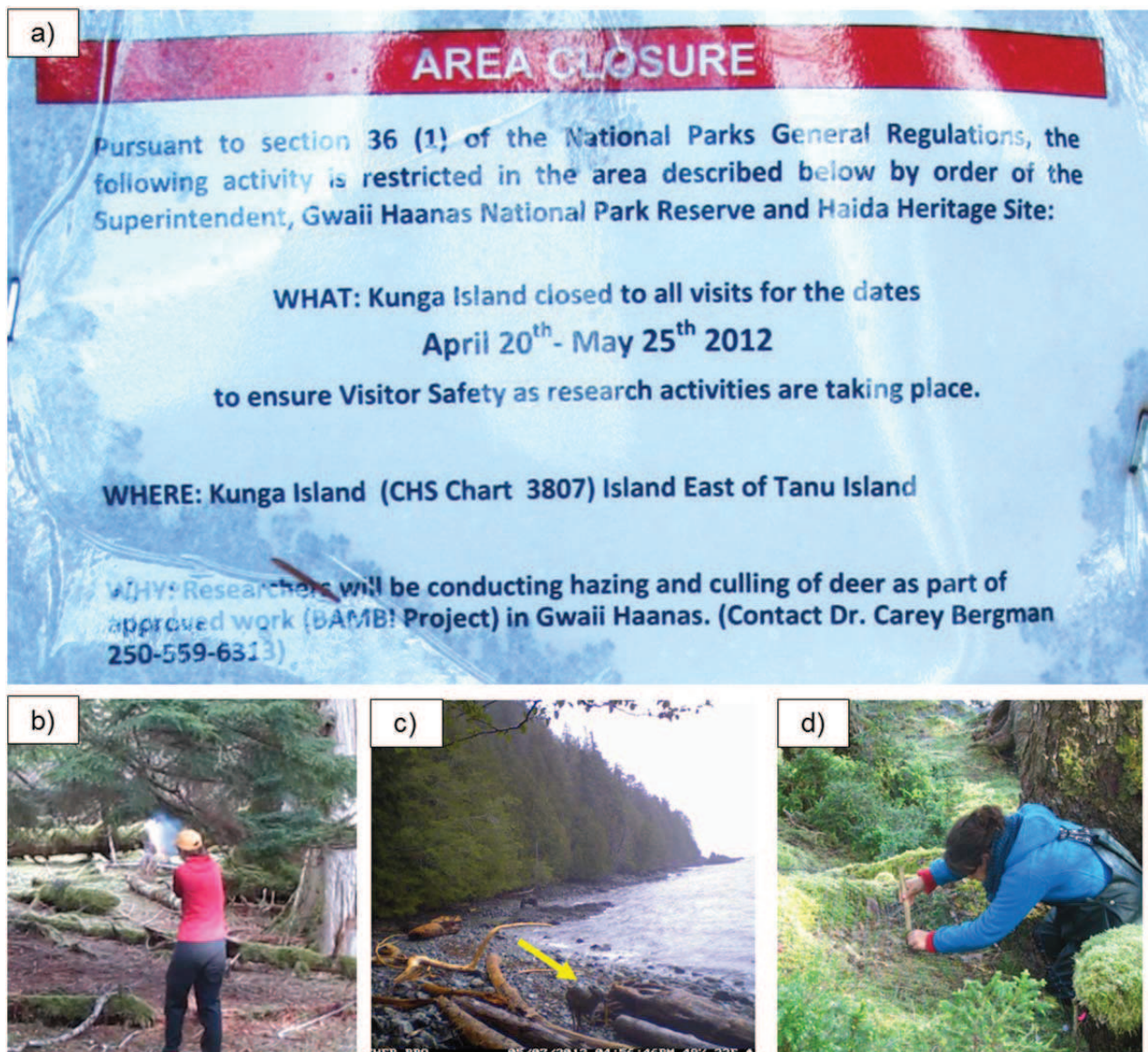


Figure F: Hunting for fear experiment on Kunga. (a) Official advertisement to prevent from touristic activity around Kunga for safety reasons. (b) Bear banger shot toward a deer in the hunting area. (c) Monitoring of deer use of the intertidal area. The yellow arrow pinpoints a deer. (d) Monitoring of plant growth outside of enclosures.

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PRELIMINARIES

Initially we designed the hunting for fear experiment to occur on the South and North coasts of Kunga and intended to use the West and East coasts as control areas. However, due to weather conditions, the North and most of the East coasts were accessible less easily. The hunting effort on the North coast was then limited. In particular, the time spent looking for deer actively was 1.4 times lower in the North than in the South coast, with an average encounter rate of deer 3 times lower in the North than in the South coast (number of scaring events/ha: North: 0.5; South: 1.5). In the North coast, only three different individuals (all marked individuals: two females and a males) were scared and an individual was killed (an unmarked buck). Given the low number of individuals scared and the low number of scaring events conducted, we could not ensure that deer could perceive changes in their environment, and hence we excluded the North coast from the analyses and considered only the South coast as hunting area.

Accessibility to most part of the East coast was more dependent from weather conditions and limited research activity. In particular, on the three other coasts (South, West and North coasts) deer were baited and/or captured between March and October 2011; however, no baiting or capture sessions occurred on the East coast prior to the hunting for fear experiment. Bait stations on the East coast were set at a distance between c. 700 and 1200 m from the closest bait stations used to study deer vigilance (Chapter III) or to capture deer on the other coasts. Black-tailed deer on Vancouver island had seasonal home ranges estimated to be between c. 15 and 150 ha (equivalent to 150- to 690-m radius circular area)(Harestad 1979). Some deer from the East coast may thus have had experienced bait in 2011 but most of them were likely bait-naïve at the beginning of the hunting for fear in 2012. Deer visits were indeed rarer on the East coast and the average frequency of deer visits at East bait stations reached less than 30% of the average frequencies of deer visits at the West and South stations. Using deer behavior at East stations as control for deer behavior in the South hunting area did not seem warranted and hence we excluded East bait stations from the analysis.

Consequently, our sample size to study deer behavioral response to the hunting for fear experiment was halved and did not allow conducting statistical analyses on fine deer behavior such as vigilance. The following chapter consists in a first set of analyses studying the effects of the hunting for fear experiment on deer behavior and its cascading effect on the coastal vegetation; and in a second set of descriptive analyses providing complementary information on deer response to the hunting for fear experiment (Complementary Analyses IV).

CHAPTER IV: MANAGING DEER-FOREST INTERACTION THROUGH FEAR: TESTING THE SHORT TERM EFFECTS OF LOW INCIDENCE HUNTING ON NAÏVE DEER.

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KEYWORDS: ungulate, large herbivore, ecology of fear, spatial behavior, trophic-cascade, predation risks, personality, trait-mediated effect, foraging behavior, browsing pressure, plant growth.

ABSTRACT

Abundant deer populations cause socio-economic and ecological concerns. Improving deer management has become a major issue. Traditionally, hunting to kill is used to reduce deer density and their impact. However, required harvest levels can be difficult or impossible to achieve. Recent awareness of non-consumptive effects of hunting on deer behavior and their cascading impact on environment, suggested “hunting for fear” as a management tool, but we need concrete tests of its power. We investigated how a predator-free black-tailed deer (*Odocoileus hemionus*) population introduced on the Haida Gwaii archipelago (Canada) responded to a hunting for fear experiment. In a restricted 21-ha area including both intertidal and coastal-forest habitats, we applied an experimental hunt that minimized killing (<2% of the estimated population) and maximized scaring deer by shooting blanks. Over 11 days of hunt spaced by 3-4 days without hunt, our hunting effort reached a level similar to other deer hunts reported. To assess potential behavioral changes resulting from this experimental hunt, we compared deer use of (1) bait stations in the forests and (2) beaches and (3) the development of four fast growing plant species (growth and browsing rate) between sites with and without hunting for fear. We predicted that deer should avoid the hunting area more at day than at night-time and that plants should grow taller in the hunting area. We showed that deer less-tolerant to human disturbance avoided the hunting area at both day and night-time. We observed no such effects in more-tolerant deer. Hunting for fear had no clear effect on how deer used beaches. Half of the plant species we studied seemed to produce more growth in the hunting area. We discuss the challenges that hunting for fear may pose to wildlife management considering the effects of hunting on phenotypic selection of the target population and its consequences for long-term management.

INTRODUCTION

In many parts of the world, local ungulate populations have dramatically increased due to the extirpation of natural predators, hunting regulations and habitat modifications (e.g. review in Reimoser 2003; Côté et al. 2004; Nugent et al. 2011). These abundant ungulate populations have considerable socio-economic impacts (e.g. reductions in the yield of sylvo-agricultural activities, increased vehicle collisions, enhanced disease transmission) as well as ecological impacts (e.g. decrease in forest biodiversity) (e.g. for deer impact see Côté et al. 2004; Takatsuki 2009; Martin et al. 2010; Beguin et al. 2010; Holt et al. 2011). Such negative impacts of overabundant ungulates have resulted in an increasing political and social demand for deer population reduction (McShea 2012; Tanentzap et al. 2012).

Hunting is commonly considered as an adequate tool to limit ungulate populations (e.g. Kilpatrick et al. 1997; Woolf & Roseberry 1998; Nugent et al. 2011; Goldthorpe & Neo 2011; Williams et al. 2012). Indeed, by its lethal effect, also referred to as consumptive effect (the direct removal of individuals), hunting seems an efficient option to reduce ungulate densities and hence their impacts (e.g. review in Milner et al. 2007). However, in practice hunting levels required to reach management goals may be difficult to achieve (e.g. Williams et al. 2012; Simard et al. 2013) and/or socially unacceptable (Garrott et al. 1993; Rutberg 1997).

If traditionally the role of hunting and predation were considered largely in simple numerical terms (number of animals killed), this view has recently been revisited. Indeed, the mere presence of predators has non-consumptive effects on ungulate behavior, as observed in deer (e.g. changes in vigilance: Benhaiem et al. 2008, in foraging behavior: Christianson & Creel 2010a or in habitat use: Bonnot et al. 2013, see Creel & Christianson 2008 for a review) which may ultimately affect deer demography (e.g. Creel et al. 2007; Creel & Christianson 2008) and their impact on the environment (e.g. Ripple & Beschta 2003; Fortin et al. 2005; Callan et al. 2013; Ripple et al. 2013).

This cascading effect of predation risk on ungulate-environment relationships through changes in ungulate behavior is at the basis of the concepts developed in the ecology of fear (Brown et al. 1999). These concepts opened new research avenues and offered, in particular, new approaches to manage abundant ungulate populations including the rehabilitation of

natural predators (e.g. Ripple & Beschta 2006; Beschta & Ripple 2007, 2010; Callan et al. 2013) or hunting (e.g. Tolon et al. 2009; Scillitani et al. 2009).

Among the range of management tools based on risk manipulation, “hunting for fear” raised a strong interest in wildlife managers and scientists. Indeed, hunting may be easier to control and manage than natural predators, and some authors also suggested that human-generated risk was stronger than risk from natural predators (Proffitt et al. 2009; Darimont et al. 2009; Ciuti et al. 2012b). The concept of “hunting for fear” led to theoretical expectations about how hunting should be implemented to maximize non-consumptive impacts of hunting on ungulates (e.g. Cromsigt et al. 2013). For example, hunting on foot or targeting juveniles may be fruitful strategies because they should allow the perception of risk by the target population by increasing the amount of cues available. Creating a spatially and temporally variable hunting landscape which maintains long-term risk perception should also contribute to maximize the non-consumptive effects of hunting on target populations (Cromsigt et al. 2013). However, most of these predictions remain to be tested in the wild and require carefully-designed protocols making it possible to disentangle between consumptive and non-consumptive effects of hunting.

Here, we tested the behavioral effect of a hunting for fear experiment on a predator-free population of black-tailed deer (*Odocoileus hemionus*) on the Haida Gwaii archipelago (B.C., Canada). We investigated how a spatially-confined hunt with limited killing but maximized scaring, affected (1) deer use of bait stations located in the forest; (2) deer use of the intertidal zone providing complementary food supply for deer (Poilvé 2013), and (3) local vegetation growth and browsing rate.

Spatio-temporal avoidance of areas used by humans is a common anti-predation strategy in hunted ungulates (Kilgo et al. 1998; Kilpatrick & Lima 1999; Sodeikat & Pohlmeier 2003; Tolon et al. 2009; Scillitani et al. 2009; Sforzi & Lovari 2011). We, thus, predicted that deer would decrease their use of bait stations in areas where hunting took place. Deer are known to also respond to temporal variation in risk and to avoid risky areas only during the period of the day that is perceived as risky (e.g. Bonnot et al. 2013). Thus, we expected that deer would use the hunting area less during the risky daytime and more during the safer nighttime. In addition, as individuals may tolerate different levels of risk (Gill et al. 2001; Bejder et

al. 2009), we predicted that deer less-tolerant to human disturbance should show exacerbated responses to the hunting for fear experiment and should avoid the hunting area even more. Finally, we expected that, in the hunting area, hunt-induced changes in deer behavior would reduce deer browsing pressure on the local vegetation (i.e. indirect effect of hunting on plants mediated by changes in deer behavior). Where hunting occurred, fast-growing vegetation should thus show increased growth and reduced browsing rate.

I. MATERIAL & METHODS

I.A. STUDY AREA

The study took place between April and June 2012 on Kunga Island (395 ha: WGS84-52.77N 131.57W), in the Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve, and Haida Heritage Site of the Haida Gwaii archipelago (British Columbia, Canada). The climate is cool temperate, oceanic, and humid-perhumid (Pojar 2008). The landscape is dominated by closed coniferous forests of western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and Sitka spruce (*Picea sitchensis*) (Pojar et al. 1980).

Black-tailed deer were introduced to the archipelago as a source of meat between 1878 and 1925 (Golumbia et al. 2008). In the absence of their main natural predators (wolves, cougars) deer populations increased and colonized most islands within 50 years. Whereas deer are hunted on the largest islands of the archipelago close to human settlements, hunting was never reported on Kunga Island, a human-free island. The island was colonized by deer about 60 years ago, and the local deer population reached high density estimated at around 45 deer/km² ([95% CI: 12 – 144], Chapter I). This abundant deer population caused a decrease of >90% of the forest understory cover when compared to deer-free islands (Martin et al. 2010; Chollet et al. in prep), with a dramatic impoverishment in most species recorded in the what is considered the typical diet of black-tailed deer (McTaggart Cowan 1956; Pojar et al. 1980). To complement their diet, deer feed on seaweed, which covers between 0 and 7% of their diet (Poilvé 2013) and spend c. 10-15% of their active daily time in the intertidal area (unpublished GPS data).

I.B. HUNTING FOR FEAR DESIGN

Under a permit delivered by the Wildlife Act of the Ministry of Natural Resource Operation of British Columbia (Permit NA11-68421), approved by Parks Canada Animal Care Task Force (Research Permit Number 9059) and by the Archipelago Management Board of Gwaii Haanas National Park reserve and Haida heritage Site (Research Permit Number GWA-2011-8373), we designed a hunting for fear protocol.

I.C. TEMPORAL AND SPATIAL EXTENT

The hunts took place during daytime between May 1 and 25, 2012 on the South coast of Kunga Island in the intertidal zone and in the coastal forest. We restricted the hunting area so that hunting never occurred at more than 100 m from the forest edge which translates into an area of about 21 ha (i.e. 5% of the island's area, Figure IV.1). By doing so we created a coastal portion of the forest where risk existed and an interior portion of the forest from which risk was absent. We used the interior forest as a local control for the use of the coastal forest. In addition we also used the West and East coasts where no hunting was applied as control areas (Figure IV.1). The portion of the island we selected as study areas had similar shoreline and sea-accessibility. Hunting consisted in two types of events: i) a large number of scaring events during which only non-lethal shooting was applied; and ii) a small number of killing events during which a restricted number of animals could be killed in order not to affect the local deer density and hence not to affect their overall pressure on the foraging resource. Killing was deemed necessary in order to introduce some level of predation risk into the predation-free study area. We decided *a priori* that a maximum of five deer could be killed during the experiment (<3% of the estimated deer population), this in order to avoid numeric impacts on the local deer population. Carcasses were left behind in the hunting area as food for scavengers (raven, eagle, rats) (Figure IV.1).

I.D. HUNTING FOR FEAR PROTOCOL

Single or pairs of hunters on foot tracked deer. They used a blank pistol firing 9mm ammunition (Margo Supply Ltd) with or without bear bangers (Pyro Banger Cartridges, 15mm, Zink Feuerwerk) for scaring events or a shotgun for killing events. When encountered, deer were approached slowly until the deer became aware of the hunter's presence (head

up, looking at the hunter) and fired at. In scaring events hunters fired blanks or bangers until the deer moved off and was no longer visible. We avoided getting closer than 10 meters to any deer when firing and aimed at c. 5 m away from the deer when using bear bangers.

We defined as a hunting session an extent of time when armed hunters looked for deer actively to potentially engage in a scaring or killing event. Hunters covered the whole hunting area at least once per hunt day. For each hunting event we recorded the number of shots fired and we sexed, aged and identified (if known from ear-tag or individual marks) the targeted deer.

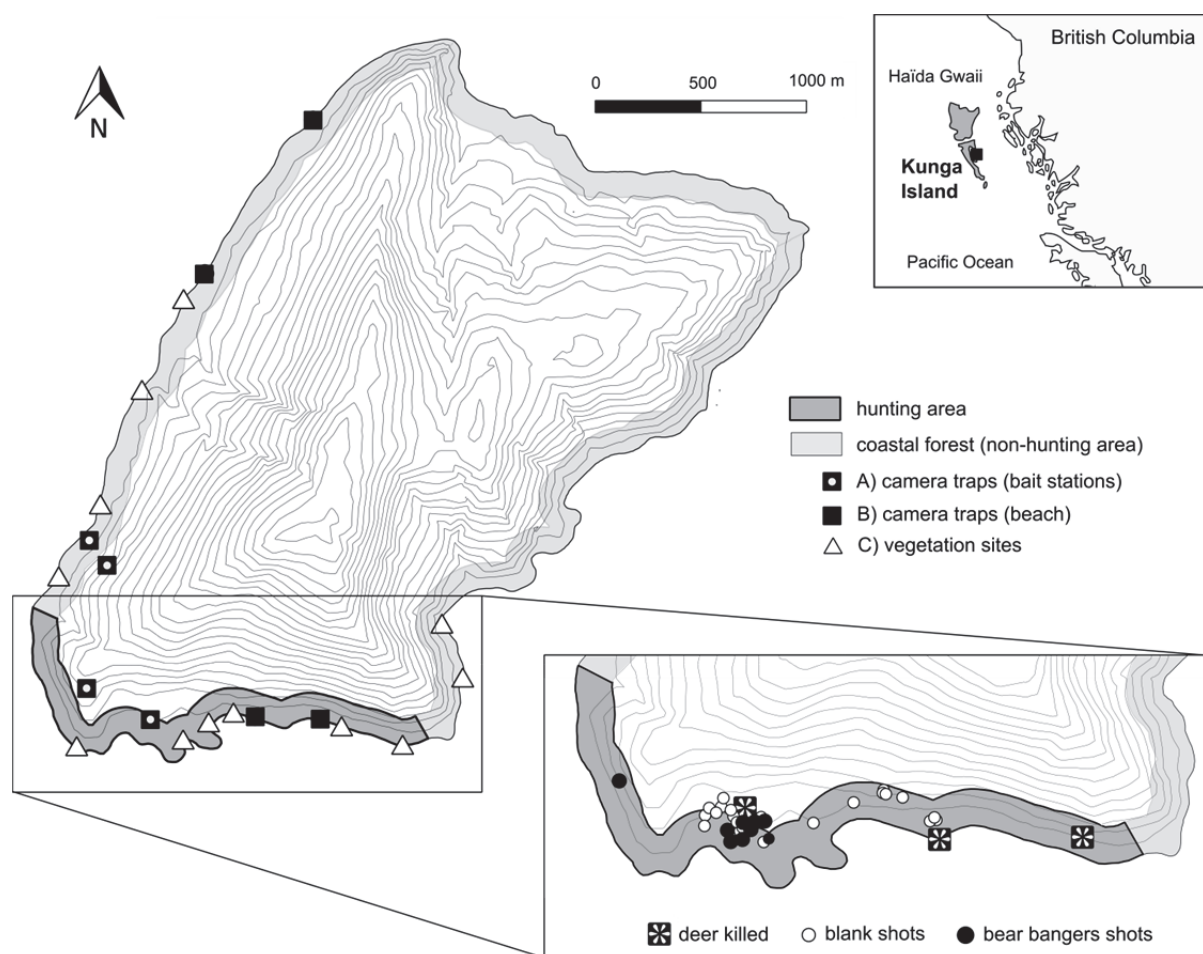


Figure IV.1: Map of Kunga Island and the hunting for fear experiment design. The dark grey area marks the hunting area, the light grey area marks the non-hunting area in the coastal forest, and the white area marks the interior forest (never hunted). Black squares with a white dot locate camera-traps to study deer use of bait stations and black squares locate camera-traps to study deer use of beaches (intertidal zone). White triangles locate vegetation sites. On the zoomed South section of Kunga, stars locate the three killing events, and circles locate the 31 scaring events (white: scaring events with blanks, black: scaring events with bear bangers).

I.E. TEMPORAL PERIODS

We identified three temporal periods: (i) the “pre-hunt” period going from April 8 to 30, defined as the 23 days before the first hunting session; (ii) the “hunt” period from May 2 to May 25, defined by the day of the first hunting event and the day of the last hunting session; and (iii) the “posthunt” period that extended from May 26 to June 17, and defined as the 23 days after the last hunting session. In addition, within the “hunt” period we identified whether the day was hunted (i.e. when at least one hunting/scaring session occurred) or not.

I.F. HUNTING FOR FEAR EFFECT ON DEER BEHAVIOR

I.F.1. DEER IDENTIFICATION

In April 2011 and September-October 2011 we organized two capture sessions on Kunga Island. Under BC Wildlife Act Permit NA11-68421, we used baited traps to capture 17 deer (10 females, 7 males) and used a net gun to capture a male. We ear-tagged deer for individual recognition. In September-October 2011 we recaptured 70% of the deer captured in April 2011. These deer were recaptured on average once every five days in September-October 2011. Other deer were commonly detected but never trapped. This suggested that marked and unmarked deer may adopt different strategies towards humans. Thus, we studied both marked and unmarked deer and predicted that unmarked deer should be more responsive to the hunting experiment and avoid the hunting area even more than marked deer.

I.F.2. DEER USE OF BAIT STATIONS

To assess changes in the spatial distribution of deer following the initiation of the hunting for fear experiment we used a design of paired-stations to bait sites equipped with automatic camera traps (Reconyx PC900). We placed one pair of stations in the hunting area (South coast) and another one in the non-hunting area (West coast). Initially, we set two paired-stations in the hunting area, but due to technical problems a paired-station stopped working and hence was removed from analysis. Each pair consisted of two stations in different habitats: we placed one station within the “coastal forest” (< 100 m from the forest edge, hunted in the hunting area only), and the other one within the adjacent “interior forest” (>200 m from the forest edge, never hunted) (Figure IV.1). Distance between the bait stations within a pair was about 150 m, a short distance for deer whose home ranges were estimated

to be c.30 ha in spring (unpublished GPS data). We thus considered that any given individual could adjust its relative use of the two stations within a pair in response to the risk perceived at the interior and coastal stations. South and West stations were c.600 m apart.

Between April 8 and June 17, we monitored deer use at each station by setting the camera-traps so as to acquire one picture per second during 99 seconds each time an animal movement triggered the motion detector. The camera-traps had a built-in infrared (IR) flash with no red glow allowing taking pictures at night. We baited the stations biweekly with 3-5 apples cut in pieces. South stations were set 10 days before West stations for logistical constraints.

We defined that a deer visit to a bait station started when the focal individual entered the camera field and ended when the deer left the camera field for more than two minutes. For each visit we recorded the date and the time of the day (day vs. night) and recorded the temporal period (i.e. “pre-hunt”, “hunt” or “posthunt”) and if the day was actually hunted.

We focused on two response variables: (i) the frequency of visits at a bait station (i.e. total number of visits per 10-minute period when the camera was active); and (ii) the proportion of visits by unmarked deer relative to the total number of visits by marked and unmarked deer. For each station and each day of active camera, we computed both variables for daytime and night-time.

I.F.3. DEER USE OF BEACHES

From April 23 to June 15, we monitored deer presence during the daytime on four beaches by using PlotWatcher Pro camera traps set at the forest edge and facing the intertidal zone. One picture was taken every 10 seconds from dusk to dawn as night-time pictures cannot be obtained from these cameras. We monitored two beaches in either the hunting area (South coast) or the non-hunting area (West coast: Figure IV.1). We considered a deer visit as the occurrence of a deer at least five minutes after the previous occurrence. Picture quality did not allow to identify deer or to detect ear tags.

For each visit we recorded the date, the time of the entry into the camera’s field and the time of exit, and recorded the temporal period in which it occurred in (i.e. pre-hunt: n=9 days, hunt: 14 non-hunted days and 10 hunted days, or posthunt: 21 days). For each day and

beach, we computed the frequency of visits as the total number of deer visits divided by the number of hours when the camera had been active.

I.G. HUNTING FOR FEAR EFFECT ON THE VEGETATION

To study whether hunting for fear could affect the vegetation, we monitored growth and browsing rate of four fast-growing plant species present in the coastal forest and heavily consumed by deer on Kunga: red huckleberry (*Vaccinium parvifolium*), Sitka spruce (*Picea sitchensis*), red fescue (*Festuca rubra*) and nootka reedgrass (*Calamagrostis nutkaensis*) (Chollet et al. 2013).

We chose sites close to the coast (<20 meters from the forest edge), where deer impact is strongest (Stockton et al. 2005, Chollet et al. 2013). Past studies have highlighted the high potential of recovery of this coastal vegetation, when deer density is reduced (Chollet et al. in prep). We monitored six vegetation sites in either the hunting area (South coast) or the non-hunting area (West coast: 4 site; East coast: 2 sites) (Figure IV.1).

In mid-April, before the beginning of the plant growing season, we built on each site a 2-m² x 1.5-m high enclosure in which we monitored the central 1-m² square. In addition, we delimited and monitored a 1-m² square outside of each enclosure. We selected at least five individuals per species in each 1-m² square inside and outside of the enclosure. For six sites we could not find a 1-m² square outside of the enclosure with five individuals for each species. For these sites (three in either hunting or non-hunting areas) we monitored an extra 1-m² square outside of the enclosure to achieve the minimum number of individuals required. In mid-April and mid-June we measured plants individually to calculate plant growth (difference in plant height between June and April). In mid-July we measured browsing rate, defined as the number of individuals browsed on the total number of individuals per plot (1-m² square). This measure did not integrate the intensity of browsing endured by each individual. Only plots with more than ten individuals were kept for the browsing rate analysis.

I.H. STATISTICAL ANALYSES

I.H.1. HUNTING FOR FEAR EFFECT ON DEER USE OF BAIT STATIONS

To study the effect of hunting for fear on deer use of bait stations, we considered the frequency of visits at bait stations and the proportion of visits by unmarked deer as response variables. For each response variable we fitted a generalized linear mixed model with a beta distribution for errors, including the area (hunting vs. non-hunting), the habitat of the station (coastal vs. interior forest), the temporal period (pre-hunt, non-hunted days of the hunt period, hunted days, and posthunt period), the period of the day (day vs. night), and all interactions as fixed effects (i.e. full model). To verify the model hypotheses we used the frequency of visits per 10-min period but used the frequency of visits per 1-hour period in graphs.

I.H.2. HUNTING FOR FEAR EFFECT ON DEER USE OF BEACHES

To study the effect of hunting for fear on deer use of beaches, we considered the frequency of visits at beaches as the response variable. We fitted a general mixed linear model with a beta distribution for errors including the area (hunting vs. non-hunting), the temporal period (pre-hunt, non-hunted of the hunt period, hunted days and posthunt period), and their interaction as fixed effects. Beach was included as a random effect on the intercept.

I.H.3. HUNTING FOR FEAR EFFECT ON THE VEGETATION

To study the indirect effect of hunting for fear on coastal plants, we considered the growth and the browsing rate of four plant species as response variables. For plant growth, we fitted for each plant a mixed linear model including the area (hunting vs. non-hunting), the type of plot (inside vs. outside enclosure) and their interaction as fixed effects and the vegetation site as random effect on the intercept. For browsing rate, due to the small number of observations and their non-normal distribution, we used a one-sided non parametric Wilcoxon test to compare browsing rates between hunting and non-hunting areas.

I.H.4. STATISTICAL TEST AND COMPUTING

For all general models using beta error, we used Cribari-Neto & Zeileis' method (2010) to verify model hypotheses. For all general and/or mixed linear models, we identified significant

effects using likelihood-ratio-tests on nested models. When a categorical variable or an interaction within categorical variables was detected as significant, we compared pairwise differences among the four temporal periods within each area (hunting and non-hunting), and between areas for a given temporal period. We used Wald-test-based comparisons with Hommel's adjusted P-value to study the significance of these pairwise differences (Hommel 1988; Fox & Weisberg 2011). We accepted a 5% type I error. All analyses were conducted with R software (R Core Team 2012), the *betareg*, *glmmADMB*, *lmtest* and *car* packages (Zeileis & Hothorn 2002; Cribari-Neto & Zeileis 2010; Fox & Weisberg 2011; Fournier et al. 2012)

II. RESULTS

II.A. HUNTING FOR FEAR EFFORT

Between May 1 and 25, we hunted 11 days during daytime (5:30 – 22:00) for a total of 64.25 hours of hunting activity. We completed 34 hunting events including only three killing events (<2% of estimated deer population): a yearling female and two adult males were killed on the first, ninth and tenth hunted days, respectively. We conducted 31 scaring events on nine different individuals: six adult females (including three marked), two adult males (including one marked) and one unmarked yearling. On Kunga deer density was estimated to be 43 deer/km² ([95% CI: 11; 136] Chapter I). The number of deer expected in the hunting area (21 ha) should be nine individuals [95% IC: 2; 28]. This coarse estimation suggests that more than a third of the local population could have been scared. Each deer was scared on average 3.8 times, but 33% (n=3) of them were scared only once and 33% of them >5 times (all marked deer). Killing events involved only a single shot, scaring events involved on average 2.7 ± 1.7 shots (blanks and/or bear bangers).

II.B. EFFECTS ON DEER BEHAVIOUR

II.B.1. FREQUENCY OF VISITS AT BAIT STATION

The frequency of visits was on average 1.6 times higher in the hunting area (mean \pm sd = 0.24 ± 0.29 visits/h) than in the non-hunting area (0.15 ± 0.20 visits/h), especially during the pre-hunt period when the frequency of visits was over 3 times higher in the hunting than in the non-hunting area (Figure IV.2 A). In the hunting area the frequency of visits remained

constant across the temporal periods (Figure IV.2 A). In the non-hunting area the frequency of visits was multiplied by 3 between the pre-hunt and the non-hunted days of the hunt period ($X^2=17.7$, $P<0.001$). Although not statistically significant, the frequency of visits was also doubled between the pre-hunt and the hunted days ($X^2=4.05$, $P=0.178$) and between the pre-hunt and the posthunt period ($X^2=4.18$, $P=0.163$) (Figure IV.2 A).

Independently from the temporal period, the stations located in the hunting areas were visited 1.8 times more often at day- than at night-time ($X^2=25.7$, $P<0.001$) contrary to the stations located in the non-hunting areas which were visited 2.5 times less often at day than at night-time ($X^2=10.6$, $P=0.005$: Table IV.1, Figure IV.2 B). In addition, independently from the temporal period and from the area, coastal stations were 1.2 times more visited at night than at daytime ($X^2=25.7$, $P<0.001$), contrary to the interior-forest stations which were visited 1.8 times more often at day than at night-time ($X^2=64.5$, $P<0.001$: Table IV.1, Figure IV.2 C).

Table IV.1: Statistics of the models on the frequency of visits at bait stations. The effects of the explanatory variables (area, temporal period, period of the day and habitat) and their interactions on the frequency of visits at bait stations were tested using a likelihood-ratio test comparing a reference model (which included the effect studied) with a focus model (which did not include the effect). See text for details. Log-likelihoods of the models, X^2 of the focus model, and P-values are presented. Significant effects are in bold.

Explanatory Variable Tested	Reference Model: model with the 4 main variables and	LogLik Reference model	LogLik		P
			Focus model	Chisq	
Area x Temporal period x Day period x Habitat	4,3,2-way interactions	1649.9	1649.6	0.516	0.916
Area x Temporal period x Day period			1647.4	4.441	0.218
Area x Temporal period x Habitat			1648.9	1.423	0.700
Area x Day period x Habitat	3,2-way interactions	1649.6	1649.6	0.073	0.787
Temporal period x Day period x Habitat			1649.2	0.915	0.822
Area x Temporal period			1641.6	9.187	0.027
Area x Day period			1622.7	47.051	<0.001
Area x Habitat			1644.5	3.466	0.063
Temporal period x Day period	2-way interactions	1646.2	1645.2	1.925	0.588
Temporal Period x Habitat			1645.3	1.819	0.611
Day period x Habitat			1642.4	7.476	0.006

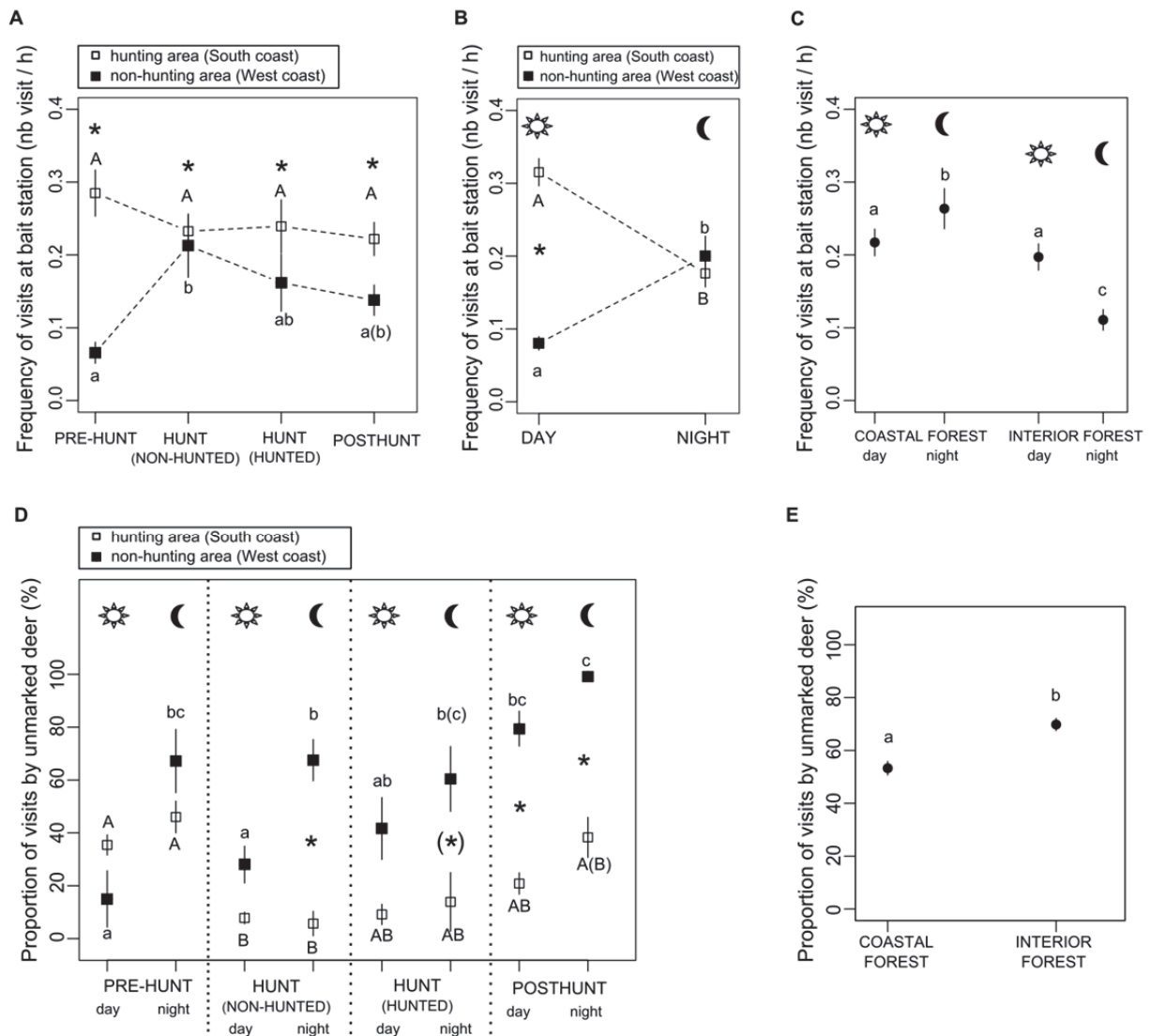


Figure IV.2: Hunting for fear effect on deer use of bait station. The frequency of visits of deer at bait stations (mean \pm standard error) is represented as a function of (A) the temporal period, (B) the interaction area x day period and (C) the interaction habitat x day period. The proportion of visits by unmarked deer (mean \pm standard error) is represented as function of (D) the 3-way interactions area x temporal period x day period and of (E) the habitat. Open squares mark the hunting area and closed squares the non-hunting area. Suns mark daytime and moons night-time. Letters identify significant differences between the frequency of visits or the proportion of visits by unmarked deer. For significant interaction involving the factor area (A,B,D), capital letters identify different levels within the hunting area, lower-case letters identify different levels within the non-hunting area, and * identify significant difference among areas (hunting vs. non-hunting) within a given temporal period. Brackets mark differences that are significant at 10% threshold only.

II.B.2. PROPORTION OF VISITS BY UNMARKED DEER

Overall, except for the pre-hunt period, the proportion of visits by unmarked deer tended to be over 2.5 times higher in the non-hunting than in the hunting area. Differences were significant during the non-hunted days at night-time and during the posthunt at both day and night-time ($X^2 > 29.0$, $P < .001$, Figure IV.2 D).

In the hunting area, the proportion of visits by unmarked deer was c. 40% during the pre-hunt period but then decreased by more than 4 times between the pre-hunt and the non-hunted days of the hunt period at day ($X^2 = 8.7$, $P = 0.048$) and at night-time ($X^2 = 12.5$, $P = 0.006$). The proportion of visits by unmarked deer also tended to decrease by more than 3 times between the pre-hunt and the hunted days, although this was not statistically significant ($X^2 < 4.6$, $P > 0.4$). The proportion of visits by unmarked deer was similar at day and at night-time for each temporal period ($X^2 < 4.4$, $P > 0.5$; Figure IV.2 D).

In the non-hunting area, the proportion of visits by unmarked deer was high (between 42 and 99%) except at daytime during the pre-hunt ($15 \pm 34\%$) and during the non-hunted days of the hunt period ($28 \pm 35\%$). The proportion of visits by unmarked deer increased by more than 5 times between the pre-hunt and the posthunt period at daytime ($X^2 = 26.8$, $P < 0.001$) and tended to increase by 1.5 times over the same period at night-time, although the difference was not statistically significant ($X^2 = 4.3$, $P = 0.572$). Visits by unmarked deer were at least 2 times more frequent at night than at day-time during the pre-hunt and the non-hunted days of the hunt period ($X^2 > 14.5$, $P < 0.002$) and were similar between day and night-time during the hunted days and the hunt period ($X^2 < 2.5$, $P > 0.999$; Figure IV.2 D).

In both areas (hunting and non-hunting), the proportion of visits by unmarked deer was higher at stations in the interior forest ($45 \pm 40\%$) than in the coastal forest ($34 \pm 39\%$; Table IV.2; Figure IV.2 E).

Table IV.2: Statistics on the proportion of visits made at bait stations by unmarked individuals. The effects of the explanatory variables (area, temporal period, period of the day and habitat) and their interactions on the proportion of visits by unmarked deer at bait stations were tested using a likelihood-ratio test comparing a reference model (which included the effect studied) with a focus model (which did not include the effect). See text for details. Log-likelihoods of the models, X^2 of the focus model, and P-values are presented. Significant effects are in bold.

Explanatory Variable Tested	Reference Model: model with the 4 main variables and	LogLik Reference model	LogLik Focus model	Chisq	P
Area x Temporal period x Day period x Habitat	4,3,2-way interactions	693.19	694.51	2.625	0.453
Area x Temporal period x Day Period			689.13	8.134	0.043
Area x Temporal period x Habitat	3,2-way	693.19	691.66	3.057	0.383
Area x Day period x Habitat	interactions		692.59	1.215	0.270
Temporal period x Day period x Habitat			692.39	1.597	0.660
Area x Habitat	Significant 3-way interaction, 2-way interactions involving habitat	690.33	689.29	2.085	0.149
Temporal period x Habitat			688.43	3.800	0.284
Day period x Habitat			689.29	2.082	0.149
Habitat	Significant 3-way interaction	687.05	682.93	8.249	0.004

II.B.3. DEER USE OF BEACHES

In the non-hunting area (Figure IV.3), the frequency of deer visits at beaches remained constant with an average value between 0.09 and 0.13 visits/h (Figure IV.3). In the hunting area (Figure IV.3), the frequency of visits during hunted days (0.069 ± 0.116 visits/h) and during the posthunt (0.080 ± 0.093 visits/h) were at least 2.8 times lower than during the pre-hunt period (0.226 ± 0.220 visits/h) and the non-hunted days of the hunt period (0.254 ± 0.378 visits/h; Figure IV.3). These results emerged from the aggregation of inconsistent dynamics at individual beaches (Appendix IV.B). In particular, individual beaches in the non-hunting area (control area) showed opposite temporal patterns that prevents their use as reliable controls for the hunting for fear experiment. We considered thus these results as inconclusive (see Appendix IV. B).

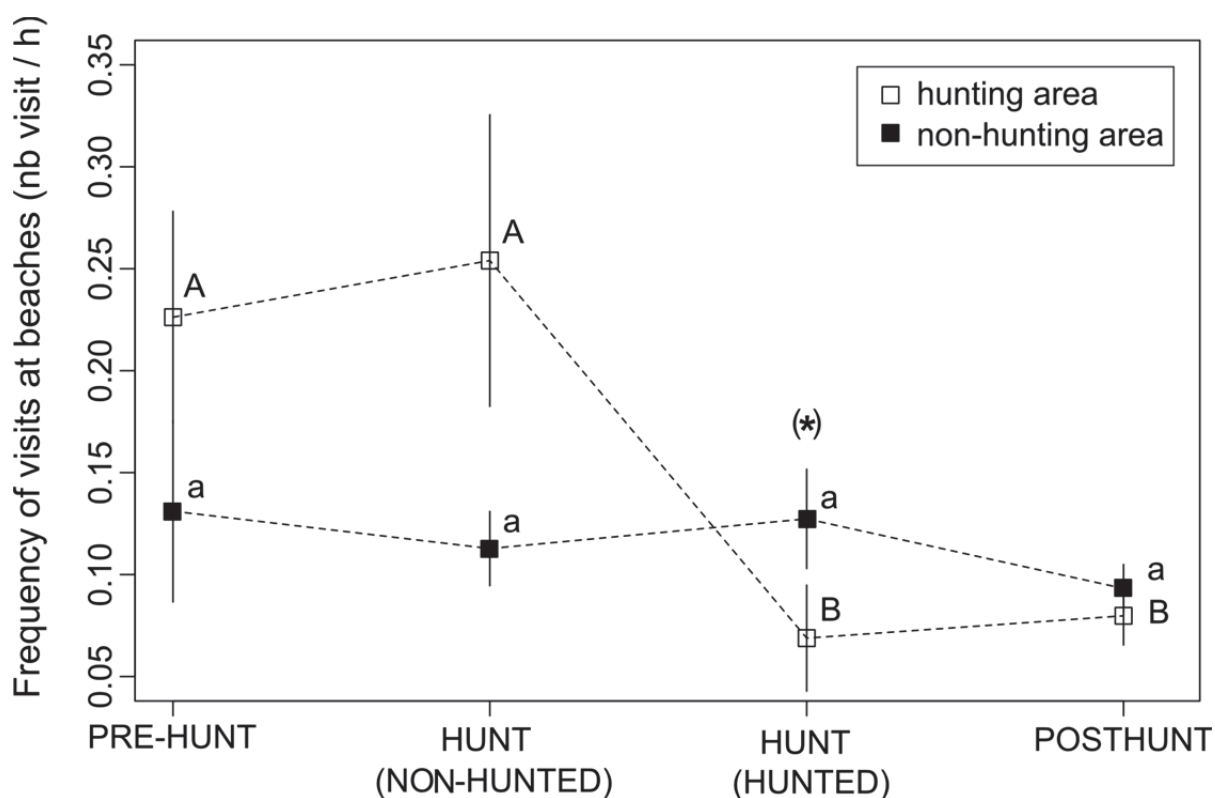


Figure IV.3: Hunting for fear effect of deer use of beaches. The frequency of visits at beaches (mean \pm standard error) is represented as function of the temporal period and of the area (hunting area: open square, vs. non-hunting area: closed square). Capital letters identify different levels within the hunting area, lower-case letters identify different levels within the non-hunting area, and * identify significant differences among area (hunting vs. non-hunting) within a given temporal period. Brackets mark differences that are significant at 10% threshold only.

II.C. EFFECTS ON THE VEGETATION

II.C.1. PLANT GROWTH

In the non-hunting area, growth was, as expected, higher inside than outside of the enclosures for the four plant species considered (Table IV.3, Figure IV.4). In the hunting area, growth was not significantly different inside and outside of the enclosures for all species except for red huckleberry, for which growth was more than 3 times higher inside than outside of the enclosures (Table IV.3, Figure IV.4).

When compared within a type of plot (inside vs. outside enclosure), the growth of red fescue and red huckleberry was similar between the hunting and the non-hunting area (Table IV.3, Figure IV.4 B,C). However, outside of the enclosures the growth of nootka reedgrass was almost twice higher in the hunting (4.12 ± 4.3 cm) than in the non-hunting area (2.31 ± 5.48 cm), whereas inside of the enclosures the growth of nootka reedgrass in the hunting area

(6.31 ± 4.52 cm) was less than half of the growth measured in the non-hunting area (14.01 cm ± 9.98; Table IV.3, Figure IV.4 A). Similarly, outside enclosure the growth of Sitka spruce was more than twice higher in the hunting area (1.35 ± 0.92 cm) than in the non-hunting area (0.61 ± 1.41 cm), whereas inside of the enclosures Sitka spruce grew similarly between the hunting and the non-hunting area (Table IV.3, Figure IV.4 D).

Table IV.3: Statistic models for the growth of four plant species. The effects of the type of plots (inside vs. outside enclosure) of the area (hunting vs. non-hunting) and their interaction on the growth of the four plant species studied are presented. Statistics χ^2 and P-values are presented for the pairwise test (see Methods) and interaction. Significant effects are in bold.

Plant species	Effect of the Interaction Area x Plot		Pairwise test : in a given area effect of the plot type inside vs. outside enclosure			Pairwise test : in a given plot type effect of the area hunting vs. non-hunting		
	χ^2	<i>P</i>	Area	χ^2	<i>P</i>	Plot type	χ^2	<i>P</i>
Nootka reedgrass	7.67	0.006	Non Hunting	41.52	<0.001	Inside	8.68	0.030
			Hunting	1.27	>0.999	Outside	8.19	0.020
Red fescue	0.72	0.39	Non Hunting	6.48	0.090	Inside	4.80	0.230
			Hunting	0.68	>0.999	Outside	0.72	>0.999
Red huckleberry	0.57	0.45	Non Hunting	22.36	<0.001	Inside	0.04	>0.999
			Hunting	13.29	0.002	Outside	0.57	>0.999
Sitka spruce	14.18	<0.001	Non Hunting	53.90	<0.001	Inside	4.92	0.200
			Hunting	0.58	>0.999	Outside	14.94	<0.001

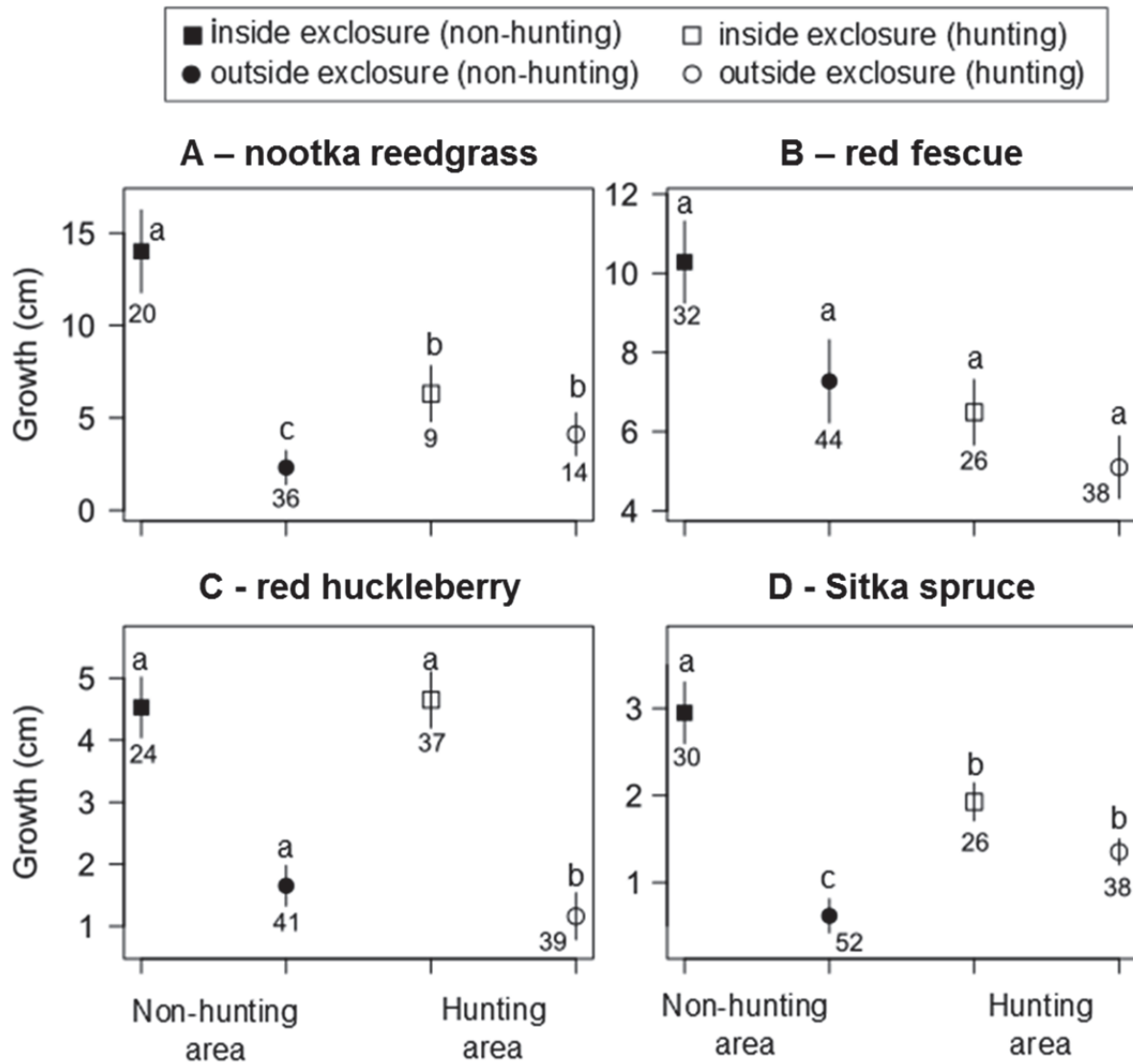


Figure IV.4: Hunting for fear effect on plant growth. Growth between mid-April and the end of June (mean in cm \pm standard error) was measured for four plant species: two grasses: (A) nootka reedgrass (*Calamagrostis nutkaensis*) and (B) red fescue (*Festuca rubra*), and two shrubs: (C) red huckleberry (*Vaccinium parvifolium*) and (D) Sitka spruce (*Picea sitchensis*), in the hunting area (open dots) and the non-hunting area (closed dots). Squares represent growth inside of enclosure, whereas circles represent growth outside of enclosure. For each species, significant difference in growth between types of plots (inside vs. outside enclosure) are identify by capital letters for the hunting area and by lower-case letters for the non-hunting area. For a given type of plot, comparisons among area (hunting vs. non-hunting) are represented by dotted lines. Numbers are the sample size.

II.C.2. BROWSING RATE

Browsing rates were not significantly different between the hunting and non-hunting areas (Wilcoxon one-sided test: $P > 0.90$ for all plants, Figure IV.5), but note that between the hunting and the non-hunting areas browsing rates of nootka reedgrass, red fescue and Sitka spruce decreased from 60 to 20%, 47 to 37% and 80 to 60%, respectively.

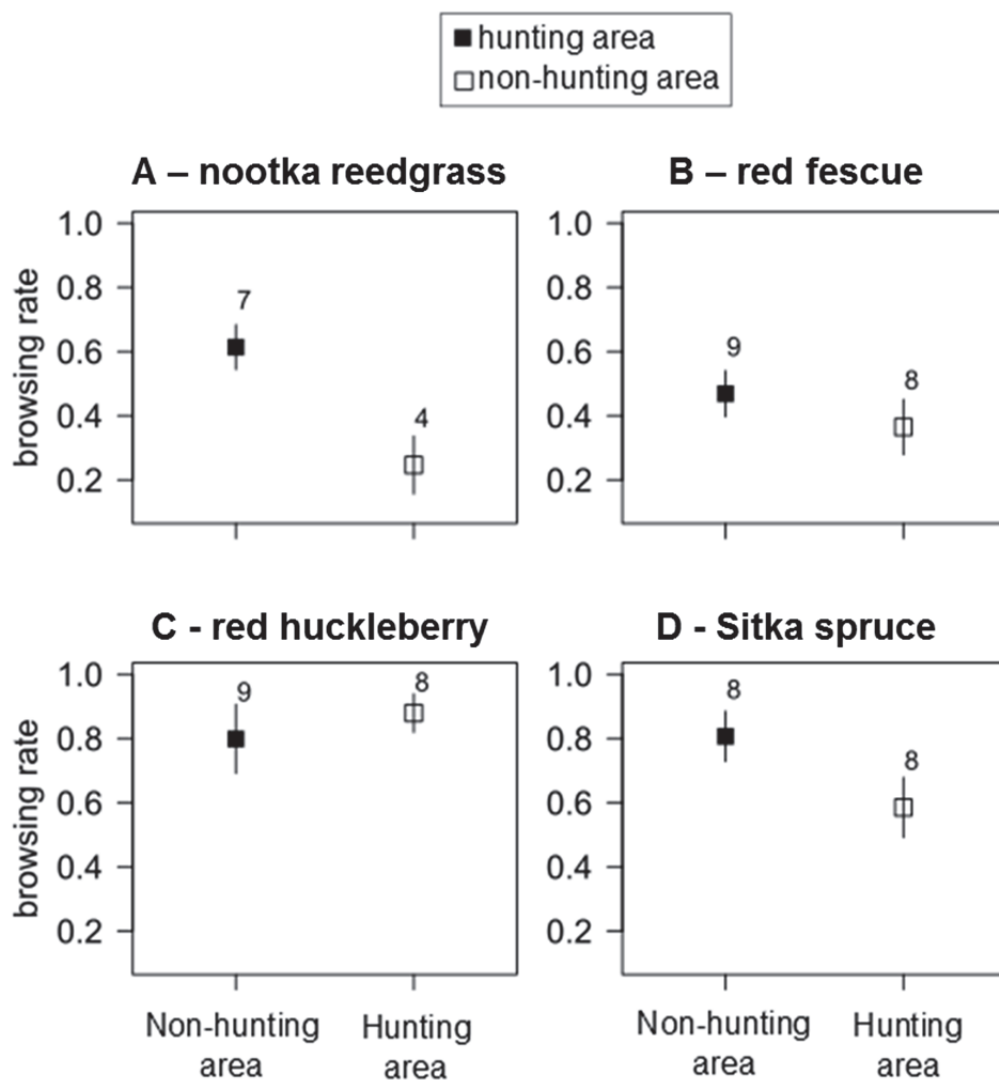


Figure IV.5: Hunting for fear effect on the browsing rate. The browsing rate (mean \pm standard error) was measured for four plant species: two grasses: (A) nootka reedgrass (*Calamagrostis nutkaensis*) and (B) red fescue (*Festuca rubra*), and two shrubs: (C) red huckleberry (*Vaccinium parvifolium*) and (D) Sitka spruce (*Picea sitchensis*). Browsing rates were compared between the hunting (open square) and the non-hunting (closed square) areas. Browsing rates were computed only for plot with > 10 total individuals. Numbers are the sample size.

III. DISCUSSION

III.A. A SIGNIFICANT HUNTING EFFORT

Over the 11 days of hunting spaced by c.2-3 days of non-hunting, we achieved an effort of 0.5-1 hunters/ha resulting in 1.48 scaring events/ha and 0.14 killing events/ha. This effort is comparable to the one reported in other hunting studies on abundant ungulate populations conducted in North America and Europe, with hunting efforts below 0.6 hunter/ha and below 1 hunting event/ha over the hunting season (review in Appendix IV.A).

III.B. DEER USE OF BAIT STATIONS: RISK AVOIDANCE BY LESS-TOLERANT DEER.

The frequency of deer visits to bait stations located in the hunting area did not decrease during the hunt (Figure IV.2 A), contrary to our expectations. However, in the non-hunting area, the frequency of visits tended to be more than doubled at both stations during the hunt. Alone, this contrasted pattern could have been interpreted as a movement of individuals from the hunting area to the non-hunting area. However, this pattern could result from an experimental bias as bait stations in the hunting area were set up 10 days before those in the non-hunting area, leaving deer with more time to find and habituate to the bait stations in the hunting area (see also Kilpatrick & Stober 2002). This seems even more probable because results for deer use of beaches were inconclusive, whereas deer response should have been even more exacerbated in this open habitat devoid of covered refuges (e.g. Kilpatrick et al. 2002; Creel et al. 2005; Bonnot et al. 2013). We thus believe that the patterns observed at bait station is more likely due to the fact that in the non-hunting area deer were still discovering the bait station after the beginning of the hunting for fear experiment on the island.

Although the total number of deer visits to bait stations in the hunting area did not decrease during the hunt, the proportion of visits by unmarked deer tended to be divided by more than three times during the hunt. On the contrary, in the non-hunting area, this proportion remained constant or even increased over the study period (Figure IV.2 D) and was detected significantly higher than in the hunting area during the non-hunted days of the hunt (at night) and the posthunt period (both at day and night-time; Figure IV.2 D). This suggests that unmarked deer avoided using the bait stations located in the hunting area during the hunt period, whereas they maintained their use of bait stations in the non-hunting areas. Thus, we

suggest that this hunting for fear experiment altered the use of bait stations by unmarked, but not marked, deer.

At least two hypotheses may explain behavioral differences between unmarked and marked deer. On the one hand, given the method of capture (baited trap), marked deer may have a lower nutritional state and hence be more prone to face risk in order to gain food (Lima & Dill 1990). However, marked deer were healthy during the capture time and did not seem to have lower body conditions than unmarked deer on pictures (pers. obs.). This hypothesis seems thus poorly supported. On the other hand, marked deer may perceive less risk than unmarked deer which in turn might be less bold and possibly more sensitive and/or responsive to human disturbances. This second hypothesis would be consistent with the observation that unmarked deer visited bait stations located in the interior forest more often than those located in the coastal forest where human activities are generally more intense (Figure IV.2 E). These coastal stations were also visited significantly more at night than at daytime, unlike interior stations (Figure IV.2 C). Finally, in the non-hunting area, mostly visited by unmarked deer, stations were also more visited at night than at day time (Figure IV.2 B). Overall, these results suggest that unmarked deer used preferentially bait stations when humans were not active in the surroundings. We thus suggest that our experiment led to different responses between individuals, depending on personality (e.g. boldness) which might have been reflected in their capturability (Gosling 2001).

III.C. HUNTING FOR FEAR EFFECT ON THE VEGETATION: A SPECIES-DEPENDENT RESPONSE

Two (nootka reedgrass and Sitka spruce) out of the four plant species studied showed a positive difference in growth between the hunting and the non-hunting area outside of the enclosures. This suggests that for these species hunting might have favored plant growth. This is supported by the unexpected observation that the difference in growth between the hunting area and the non-hunting area was negative inside of the enclosures for nootka reedgrass (and possibly also for Sitka spruce) (Figure IV.3 A,D). This suggests that the potential for growth may have been initially lower in the hunting area, a pattern that would reinforce our interpretation of a positive impact of hunting on the growth of nootka reedgrass and Sitka spruce.

However, browsing rates did not decrease significantly in the hunting area (Figure IV.4), although a trend for all species except for red huckleberry might have been hidden by the low sample size. Our index of browsing rate recorded the proportion of individuals browsed but did not account for different levels of browsing intensity endured by plant individuals. Our browsing index might therefore have been too coarse to reveal actual changes in browsing pressure due to redistribution of unmarked deer in the landscape when hunting occurred. Changes in browsing pressure could also be expected due to changes in deer vigilance levels associated with increasing predation risk (e.g. Laundré et al. 2001; Jayakody et al. 2008; Benhaïem et al. 2008). However, we could not study this effect here and hence considered that our browsing index was likely too coarse to detect subtle changes.

In addition, because browsing rate was measured a month after the hunt period, this may also imply that within a month following the hunting for fear experiment, deer came back to their initial browsing behavior. This would be in agreement with previous hunting *per se* reporting that deer came back to their initial behavior within a few days to weeks following the end of the hunt (e.g. Vercauteren & Hygnstrom 1998; Millspaugh et al. 2000; review in Sforzi & Lovari 2011). If confirmed, this would emphasize the short-term effect of our hunting for fear experiment. Whether our index was too coarse or the experiment had only a short-term impact on deer behavior or both could not be disentangled here and would need to be further explored.

Contrasted responses among plant species to the hunting for fear experiment could be explained by at least two interspecific differences in plant characteristics. First, we studied two grass species (nootka reedgrass and red fescue), a shrub species (red huckleberry) and a tree species (Sitka spruce) which differ in palatability. For example, unlike the three other species, red huckleberry is a preferred food item in the traditional diet of black-tailed deer (McTaggart Cowan 1956; Pojar et al. 1980). Deer may thus face hunting risk by focusing on foraging on this preferred species rather than on less preferred food items like Sitka spruce or nootka reedgrass (Lima & Dill 1990; Augustine & McNaughton 1998). Secondly, these four species have different growth physiologies and potentials of recovery that may lead to different response to change in browsing pressure. For instance, due to lignotuber, red huckleberry is easily maintained under high browsing pressure whereas grasses are known to have high annual growth which can be possibly stimulated by low browsing pressure

(Louda et al. 1990; Augustine & McNaughton 1998; Vila et al. 2004). This might explain the level of growth observed in nootka reedgrass. Although, the exact mechanism remains unknown, differences in both deer selectivity and plant physiology may explain the different growth patterns observed among these plants.

This species-dependent cascading effect on plants highlights the importance of defining clear management targets before considering hunting for fear as a management tool (Raik et al. 2005). Management targets would be even more crucial considering that deer browsing pressure may just have been locally and temporarily displaced to refuge areas (Proffitt et al. 2009; Orrock et al. 2012) which, according to the management targets, may or may not be an acceptable outcome. Managers should thus be cautious when using cascading effects of predation risk as management tools.

III.D. CONCLUSION: WHEN MANAGEMENT INTERACTS WITH DEER PERSONALITY

The contrasted response of marked and unmarked deer highlights the importance of considering individual variability in hunting management. Indeed, the distribution of individual variability in a population interacts with management practices to define strength and direction of selection (reviewed in Mysterud 2011). For example, in the Rocky Mountains, Alberta, Canada, Ciuti et al (2012a) reported that hunting could select-against fast-moving elk (*Cervus elaphus*) because more active deer were more likely to be detected and killed by hunters, especially if they used open areas. Deer are able to learn and adjust their behavior in presence of predation risk (e.g. Ozoga & Verme 1986; Berger et al. 2001). However, most of the time whether predation- or human-induced changes in the distribution of behavioral types are due to selection or phenotypic plasticity of these labile traits remains an open question (e.g. Frair et al. 2007; Ciuti et al. 2012a). Both are known to occur (e.g. Hendry et al. 2008; Darimont et al. 2009; Sih et al. 2011; Ciuti et al. 2012b; Sih 2013) and should thus be considered as possible outcomes of wildlife management activities.

Our study suggests that behavioral flexibility has limits which might ensure that selection for less bold phenotypes occurs. In our situation the lack of response of marked deer to the hunting for fear experiment might be due to a too short period of hunting for fear (11 days of hunting spread over 25 days) to allow predator-naïve deer to learn and adjust their

behavior. It would thus be interesting to see how deer would respond to longer and/or repeated hunting for fear experiment. However, the fact that these deer could be easily recaptured and re-handled during capture session raises the question whether scaring events may effectively alter their behaviors. In addition, despite about 60 years of absence of lethal perturbation by humans on Kunga, some deer have remained so cautious as not to enter in traps baited with a likely much-needed resource. Both observations suggest that at least part of this behavioral trait (boldness) is inherited. Because hunting is expected to favor individuals which are less-tolerant towards hunting and humans, in our situation marked individuals are likely to be removed if hunting is maintained and if they cannot learn. This raises then the question of how the response of less-tolerant individuals would evolve (or not) over time should the hunting/scaring pressure continue. In particular it appears critical to understand if the response would strengthen as individuals learn to recognize earlier the cues indicating changes in risk levels. If so, individuals would be able to quickly adjust space use to the management practices (e.g. Vercauteren & Hygnstrom 1998; Millspaugh et al. 2000; Sodeikat & Pohlmeier 2003; Proffitt et al. 2009; Kamei et al. 2010), and maintenance of very regular disturbances would be required to be effective (Kilpatrick et al. 2002; Croomsigt et al. 2013). If not, then selection for less bold phenotype would continue, likely leading to the selection of individuals spending much time using refuge areas. This could lead to earlier expression of density-dependence (Preisser et al. 2009; Orrock et al. 2012) and free some areas from significant browsing pressure. These remain tentative scenarios however. They remain to be tested more directly to predict how efficient hunting for fear would be in places where hunting has already been taking place.

To conclude, this simple hunting for fear experiment highlighted that predation risk could mitigate deer impact on some plant species, and this was likely mediated by the avoidance of the hunting area by the deer individuals the least-tolerant to human disturbance and hunting. This raises the concern of human-induced changes in animal phenotypic traits and their necessary consideration in any management plans involving changes in animal behavior and/or removal of individuals. In particular, whether deer or more generally target individuals switch temporarily or permanently to refuge areas may lead to different outcomes which are likely to affect both management strategies and the ecological and

evolutionary future of the target populations and of their relationship with their environment (Wolf & Weissing 2012; Sih 2013).

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APPENDIX IV.A. EXAMPLE OF HUNTING REPORTED IN THE LITERATURE AND CONDUCTED ON ABUNDANT UNGULATE POPULATIONS

We reviewed seven studies from North America and Europe that reported sufficient data to estimate various metrics of hunting effort on abundant ungulate populations. We detailed below how these were calculated and results are presented in Table IV.A.1. In Fair Hill Natural Resource Management Areas (Maryland, U.S.), Ebersole (2006) reported several seasons of controlled hunts on white-tailed deer (*Odocoileus virginianus*). They occurred on an area >900 ha during 2-6 day per season and involved 85 hunter/day. This led to a total effort of 0.19 to 0.57 hunter/ha over a given season. Cleveland (2010) studied the effect of hunting on elk (*Cervus elaphus*) in Missoula County (Montana, U.S.) where hunting seasons of 5- 6-week may involve up to 100 hunters/week. No detailed information on the area over which hunts occurred was provided. Assuming that most of the hunts were conducted in forest areas of this county ($\geq 2500 \text{ km}^2$), this would represent a hunting effort of less than 0.0025 hunters/ha. In Southeastern Alaska, Johnson & Wood (1979) reported that residents of Sitka harvested about 1400 black-tailed deer within a 30 miles radius of the town, let a harvest rate of 0.002 deer/ha over a year. They also reported that Juneau hunters harvested about 2000-5000 black-tailed deer among which 60% came from Admiralty Island (4264 km^2), let a rate of 0.003-0.007 deer/ha over a year (Johnson & Wood 1979). In Europe Scillitani et al. (2009) conducted an experimental hunt on wild boar (*Sus scrofa*) in Northern Apennines (Italy) which involved 0.25 hunters/ha and achieved average harvest rates of 0.025 ± 0.045 wild boar/ha over a given hunting season. Considering that in our experiment the effort was of 0.5-1 hunter/ha and 1.48 scaring events/ha over the hunting season, we concluded that we created a hunting level comparable to those experienced by hunted ungulates in other situations.

Table IV.A.1: Estimation of hunting effort reported in seven studies in comparison to the hunting effort reached in the present study. The reference (Ref.), the species hunted, the site area (ha), the duration of the hunting season, the number of hunters (nb hunters), the hunt effort (number of hunters/ha over the hunting season) and the hunting effort (number of hunting events/ha over the hunting season) are provided.

Ref	Species	Site area (ha)	Hunting season duration	Nb hunters	Hunt effort (nb hunter/ha)	Hunting effort (nb events/ha)
1	White-tailed deer	> 900	2-6 day	85/day	0.19-0.57	NA
2	Elk	≥ 250000*	5- 6-week	≤ 100/week	0.0025	NA
3	Black-tailed deer	723800	NA	NA	NA	Killing event : 0.002
3	Black-tailed deer	426400	NA	NA	NA	Killing event : 0.003-0.007
4	Wild boar	NA	NA	NA	0.25	Killing event : 0.025 ± 0.045
5	Black-tailed deer	21	11 day	1-2/day	0.5-1	Killing event : 0.14 Scaring event :1.48

*area estimated, considering that hunting effort focused mainly in forest areas within Missoula County

1: Ebersole 2006; 2: Cleveland 2002; 3: Johnson & Wood 1979; 4: Scillitani et al. 2010; 5: present study

APPENDIX IV.B. DEER USE OF BEACHES – SITE EFFECT

To study the effect of the hunting for fear experiment on deer use of beaches for each beach individually (beached in the hunting area : B1,B2 ; in the non-hunting area : B3,B4) we fitted a generalized linear model with a beta distribution for errors and with the temporal period (pre-hunt period, non-hunted days and hunted days during the hunt, posthunt period) as explanatory variable. We removed an observation according to Cook's distance (Cook distance $> 2*4/n$) for beaches B1, B2 and B4.

In the non-hunting area (beaches B1,B2), the frequency of visits through time was contrasted among beaches. At the beach B1, the frequency of visits did not depend on the period of hunting ($X^2=2.54$, $P=0.47$). But there was an overall decrease of $>50\%$ from the pre-hunt to the posthunt period, although not significant ($X^2\leq 2.57$, $P\geq 0.11$; Figure IV.B.1 B1). Conversely, at the beach B2, the frequency of visits depended on the period of hunting ($X^2=19.89$, $P<0.001$). There was an increase of $>80\%$ from the pre-hunt to the posthunt period (pre-hunt vs. non-hunted days: $X^2=9.11$, $P=0.004$; pre-hunt vs. hunted days: $X^2=19.64$, $P<0.001$; pre-hunt vs. posthunt: $X^2=6.27$, $P=0.01$; non-hunted days vs. hunted days: $X^2=5.14$, $P=0.02$; hunted days vs. posthunt: $X^2=9.51$, $P=0.002$; Figure IV.B.1 B2).

In the hunting area (beaches B3 and B4), changes in the frequency of visits were not consistent among beaches. At the beach B3, the frequency of visits was slightly impacted by the hunt period ($X^2=6.56$, $P=0.09$). There was a significant decrease of 70 % between the non-hunted days and the hunted days of the hunt period ($X^2 = 3.98$, $P=0.04$, Figure IV.B.1), and between the non-hunted days of the hunt period and the posthunt period ($X^2 = 6.19$, $P=0.01$). However, this pattern was not observed at the beach B4, which instead presented a pattern comparable to beach B1 with no effect of the period of hunting ($X^2=2.31$, $P=0.52$; Figure IV.B.1 B1, B4). Although the pattern observed in the hunting area at the beach B3 differed from the ones observed in the non-hunting area (beaches B1, B2), this pattern was not consistent among beaches in the hunting area either. The hunt had thus no clear effect on deer use of beaches.

From a conservative viewpoint, we considered that the decrease of 60% observed in the averaged frequency of visits at beaches in the hunting area resulted from two contrasted patterns which could not be generalized. Thus, we concluded that the hunt had no strong

effect on the frequency of visits of beaches, and if the hunt had an effect this should still be demonstrated.

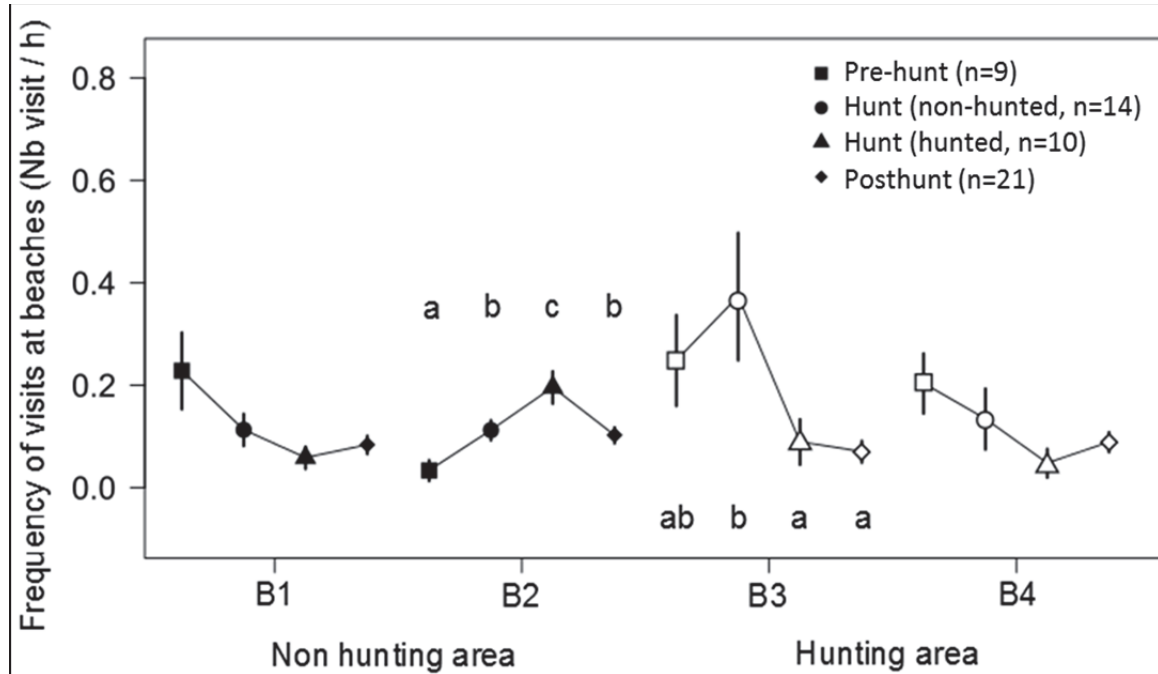


Figure IV.B.1: Hunting for fear effect on deer use of each individual beach site. The frequency of visits (number of visits per hour, mean \pm standard deviation) is plotted for each individual beach in the non-hunting area (in grey: beaches B1 and B2) and in the hunting area (in black: beaches B3 and B4), with squares for pre-hunt period; circles for non-hunted days during the hunt period, triangles for hunted days and lozenges for the posthunt period. Letters identify significant differences in the frequency of visits of a given beach (Post hoc test).

COMPLEMENTARY ANALYSES IV

CA.IV. DID THE HUNTING FOR FEAR EXPERIMENT AFFECT DEER PHYSIOLOGICAL STRESS RESPONSE, VIGILANCE, FLIGHT DISTANCE, ACTIVITY PATTERN AND HABITAT USE?

In addition to the previous analyses we also collected various data on deer physiological state and deer spatio-temporal behavior. Sample sizes were limited and no sensible statistical analyses could be conducted, but they provided interesting insights on deer response to the hunting for fear. The qualitative results obtained are described below.

We considered five indices to assess if and how the hunting for fear may affect deer: 1) the level of fecal glucocorticoid metabolites (FGM); 2) deer overt vigilance; 3) flight distance; 4) deer activity pattern through indices of diurnality, movement rate, and of synchronization with the circadian cycle; and 5) deer habitat use in their seasonal home range.

For each analysis, excluding vigilance, we had access to four datasets: i) data from April-June 2011 in the hunting area on Kunga (a year before the hunting for fear); ii) data from April-June 2012 in the hunting area on Kunga (the year of the hunting for fear); iii) data from April-June 2011 on East Limestone; and iv) data from April-June 2012 on East Limestone. For each dataset we could identify at least three temporal periods: the pre-hunt, the hunt and the posthunt periods. We investigated the effect of the hunting for fear on deer physiology and behavior in comparing the temporal trend over these three periods. Because seasonal variations may affect this pattern, we used three controls as reference patterns: a diachronic (Kunga in 2011), a synchronic (East Limestone in 2012) and a contextual control (East Limestone 2011). This offered three temporal dynamics to compare with the one observed in the hunting area during the hunting for fear “treatment” in 2012 (Table CA.IV.1).

Table CA.IV.1: Design to explore the effect of the hunting for fear experiment on deer physiological stress response and deer behavior. The role of each dataset is presented according to the island (East Limestone and Kunga) and to the year (2011 and 2012) considered. The “treatment” is highlighted and italic.

Island \ Year	April-June 2011	April-June 2012
East Limestone	Contextual control	Synchronic control
Kunga (hunting area)	Diachronic control	<i>Treatment :Hunting for fear</i>

To study deer vigilance, we used data obtained in April-June 2012 on East Limestone and on Kunga in the non-hunting (West) and the hunting (South) areas. Vigilance data came from the dataset to study deer use of bait station (Chapter IV). A similar design was used on East Limestone with bait stations set either in coastal or interior forest. For this particular case, we had thus access to five controls: a local control within the hunting area (interior habitat); a control in either habitat (interior and coastal habitats) at the scale of the island in the non-hunting area on Kunga; and two contextual controls on East Limestone in either habitat (Table CA.IV.2).

Table CA.IV.2: Design to explore the effect of the hunting for fear experiment on deer vigilance. The role of each dataset is presented according to the island and area considered (East Limestone, non-hunting and hunting areas on Kunga) and to the habitat considered (interior and coastal forest). The hunting for fear “treatment” is highlighted and italic.

Island: area \ Habitat	Interior Forest	Coastal Forest
East Limestone	Contextual control	Contextual control
Kunga : Non-Hunting area (West)	Control at the island scale	Control at the island scale
Kunga : Hunting area (South)	Control at the local scale	<i>Treatment: Hunting for fear</i>

The distinction between interior and coastal forest was possible only for vigilance and flight distance measurements. For all other indices we considered the hunting area as the risky area.

CA.IV.A. DEER PHYSIOLOGICAL STRESS RESPONSE TO THE HUNTING FOR FEAR EXPERIMENT

I. PREDICTION

Because in presence of predation risk animals are expected to mount a stress response (e.g. Boonstra et al. 1998; Clinchy et al. 2004), we expected deer fecal glucocorticoid metabolite levels (FGM levels) to peak during the hunt in the hunting area.

II. MATERIAL & METHODS

We studied deer physiological stress response by measuring FGM levels in samples collected in April, May and June 2011 and 2012 on East Limestone and in the hunting area on Kunga (Table CA.IV.3). We followed exactly the same method as described in Chapter II to collect, store and to assay FGM levels. For each month we calculated the average FGM levels and compared the temporal pattern obtained for each conditions (East Limestone 2011, East Limestone 2012, Kunga 2011 and Kunga 2012: Table CA.IV.1)

Table CA.IV.3: Sample size available to study the effect of the hunting for fear experiment on deer physiological stress response. Sample size for the treatment condition (Kunga 2012) are highlighted and italic.

Island – Year	April	May	June
East Limestone – 2011	10	10	10
East Limestone – 2012	9	10	10
Kunga: hunting area – 2011	0	3	6
<i>Kunga: hunting area - 2012</i>	6	5	5

III. RESULTS & DISCUSSION

On both islands, FGM levels assessed in 2012 were overall similar to those measured in 2011 (Figure CA.IV.1). No major peak was observed in the hunting area during the hunt (May 2012). This dataset seems to suggest that deer did not develop chronic physiological stress in response to the hunting for fear experiment on Kunga. Further analyses are required to confirm this result, however, if true, this would support the results assessed in Chapter II, according to which deer may mitigate their exposure to stressors in avoiding risky area. This strategy was indeed observed in less-tolerant deer which left the hunting area (Chapter IV). Deer remaining in the hunting area might perceive fewer disturbances and remain in the hunting area without developing chronic stress. This, however, should be confirmed.

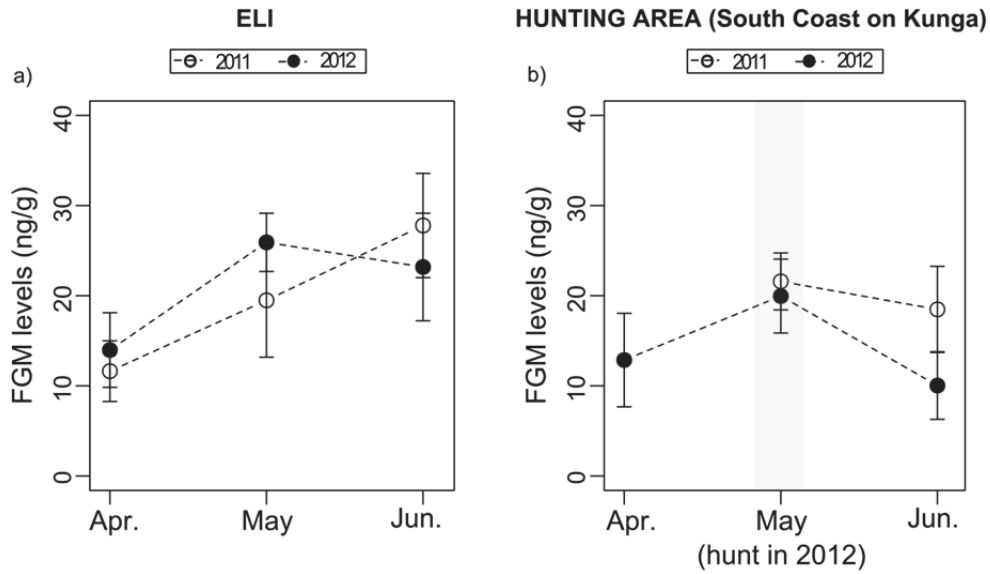


Figure CA.IV.1: Physiological response of deer to the hunting for fear experiment: Fecal glucocorticoid metabolite levels (FGM levels) assessed in April, May and June 2011 (open dots) and 2012 (closed dots) on East Limestone (a) and Kunga (b) are presented. The hunting for fear experiment took place on Kunga in May 2012 (grey area).

CA.IV.B. DEER VIGILANCE IN RESPONSE TO THE HUNTING FOR FEAR EXPERIMENT

I. PREDICTIONS

Deer can manage risk temporally and/or spatially (Brown 1999). Two alternative predictions may thus be considered. On the one hand, deer may manage risk temporally. As risk increased during the hunt period, deer would be expected to invest more time in vigilance (Lima & Dill 1990). On the other hand, deer may manage risk spatially and limit their use of the risky area. In this case, deer would be expected to minimize their time in the hunting area and to maximize their intake when present in this risky area. Under this scenario deer would be expected to invest less time in vigilance during the hunt. Such a strategy was reported in Idaho, U.S., where mule deer spent less time in the more risky area but did not invest more time in vigilance (Altendorf et al. 2001). Because hunt occurred at daytime, if deer adjusted their vigilance levels this should be exacerbated at daytime.

II. MATERIAL & METHODS

II.A. EXPERIMENTAL DESIGN

We used the experimental design set to study deer use of bait station during the hunting for fear experiment (Chapter IV). A similar design was set concomitantly on East Limestone. We could thus study deer overt vigilance between May and June 2012 at bait stations set in the coastal and interior forest on East Limestone and in the non-hunting and hunting area on Kunga (Table CA.IV.2). We considered two temporal periods: the pre-hunt (from March 26 to April 30) and the hunt (from May 2 to June 1) periods. Although the hunt experiment ceased on May 25, we extended the hunt period to study deer vigilance up to May 28 on Kunga (where the hunt occurred) and to June 1 on East Limestone (control area). We assumed that, if deer responded to the hunting for fear experiment, these changes may last a few days (Vercauteren & Hygnstrom 1998; Kamei et al. 2010). This allowed us to implement our limited dataset.

We selected picture sequences in a similar way as described in Chapter III. In particular, we considered only sequences when individuals were alone at the bait station and spent at least two minutes within reach of the bait. As deer vigilance levels were affected by the period of day, we considered both day- and night-time, excluding twilight periods (within 15 minutes of the civil sunset and sunrise). Because bait had a low to negligible effect on deer overt

vigilance levels (Chapter III), in this analysis we pooled all bait levels together. For each temporal period (pre-hunt vs. hunt) and period of the day (day vs. night) in each habitat (coastal vs. interior forest) and each area and island (East Limestone, non-hunting area on Kunga and hunting area on Kunga) we analyzed the first sequence that matched the above criteria. This resulted in 129 sequences accounting for a total of 15 individuals on East Limestone, 5 in the non-hunting area on Kunga and 8 in the hunting area (Table CA.IV.4)

II. B. ANALYSES

For each sequence we calculated the proportion of time spent in overt vigilance (hereafter vigilance) over the first two minutes spent within reach of the bait. We compared the temporal pattern of deer vigilance between the five control situations and the treatment situation (Table CA.IV.2) at day- and night-time. In addition, because visibility may impact deer vigilance levels at night (Chapter III), we also studied the average visibility level at the stations visited at night in each habitat in each area and during each temporal period.

Table CA.IV.4: Sample size to study the effect of the hunting for fear experiment on deer vigilance. The number of individuals is provided for each habitat in each area, during each temporal period (pre-hunt and hunt) and during the period of the day considered (day vs. night). Sample sizes for the treatment condition (coastal forest in the hunting area) are highlighted and italic.

Area -habitat	PRE-HUNT		HUNT	
	Day	Night	Day	Night
East Limestone – coastal Forest	11	9	5	4
East Limestone – interior Forest	10	12	5	2
Kunga : non-hunting area – coastal Forest	3	1	2	3
Kunga : non-hunting area – interior Forest	1	2	2	1
<i>Kunga : hunting area – coastal Forest</i>	4	3	3	2
Kunga : hunting area – interior Forest	6	1	4	1

III. RESULTS & DISCUSSION

On East Limestone, deer vigilance levels were similar between temporal periods, although at daytime they tended to increase from 8 to 11% in the coastal forest and to decrease from 15 to 11% in the interior forest (Figure CA.IV.2 a). At night-time average visibility levels at the stations visited were fairly constant as well as the overt vigilance levels (Figure.CA.IV.2 d).

On Kunga, deer vigilance patterns were opposite between the non-hunting and the hunting area. In the non-hunting area, deer vigilance levels were divided by more than a half between the pre-hunt and the hunt, except at night-time in the interior forest when they remained fairly constant (Figure.CA.IV.2 b). In the hunting area, deer vigilance levels were doubled between the pre-hunt and the hunt, except at day-time in the coastal forest when they were divided by 5 (Figure.CA.IV.2 c). Changes in visibility at night is unlikely to account for these pattern as it remained constant in the non-hunting area (Figure.CA.IV.2 e) and increased in the hunting-area, which should have been linked to a decrease in vigilance levels (Figure.CA.IV.2 f).

These contrasted patterns should be validated because sampling artifacts may occur (Table CA.IV.4). However, the marked increase in deer vigilance in the hunting area associated with a marked decrease in vigilance level at daytime at coastal stations is striking (Figure.CA.IV.2 e). If validated, this would suggest that deer in the hunting area became more vigilant during the hunt, expect in the more risky area (coastal station) where they reduced their vigilance levels. At the coastal station, vigilance levels dropped of 10% during the hunt, whereas the proportion of time spent at the ground level increased of 11% and the proportion of time spent grooming did not change. This suggests that deer re-allocated their time in favor of foraging activities in the riskier area. If true, this would support our results assessed in Chapter III.2, according to which deer manage risk spatially and limit their exposure to predation risk. It would be interesting to validate this result because, as unmarked deer left the hunting area (Chapter IV), this result would suggest that marked deer, considered as more-tolerant to humans, might have perceived some risk in presence of the hunting for fear experiment and might be able to adjust their foraging behavior accordingly. An interesting complementary index to confirm this kind of spatio-temporal management of risk by deer would have been to use giving-up density.

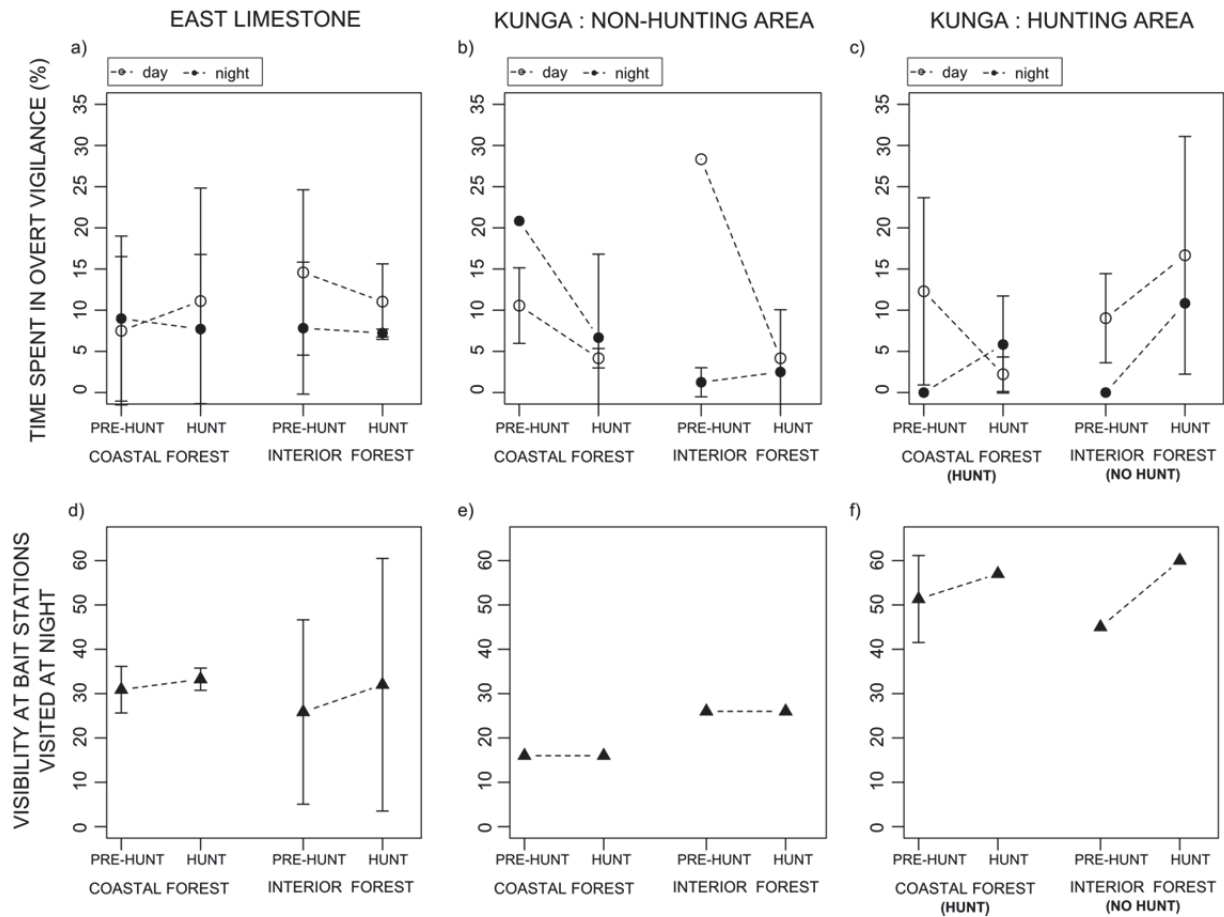


Figure CA.IV.2: Effect of the hunting for fear experiment on deer overt vigilance levels on East Limestone (a,d),in the non-hunting area on Kunga (b,e) and in the hunting area on Kunga (c,f). The proportion of time spent in overt vigilance (mean \pm sd : a,b,c) was provided for each habitat (coastal vs. interior forest) during each temporal period (pre-hunt vs. hunt). Open dots marked daytime and close dots marked night-time. In the hunting area, deer were hunted only in the coastal forest (Table CA.IV.2). The average visibility level (mean \pm sd: triangle) of the stations visited in a given habitat during a given temporal period at night-time was provided for each island and area (d,e,f).

CA.IV.C. DEER FLIGHT DISTANCE IN RESPONSE TO THE HUNTING FOR FEAR EXPERIMENT

I. PREDICTIONS

All other things being equal, in presence of predation risk, deer should increase their flight distances (e.g. Grau & Grau 1980; Stankowich & Coss 2005; Kloppers et al. 2005; Stankowich 2008). We thus expected deer to increase their flight response during the hunt in the hunting area. This was even more expected in the more risky coastal forest and for unmarked deer, assumed to be more sensitive to human disturbance (Stankowich & Blumstein 2005).

II. MATERIAL & METHODS

II.A. EXPERIMENTAL DESIGN

We conducted flight distance experiments in May-June 2011 and in late April -early July 2012 on East Limestone and in the hunting area on Kunga. All measurements were conducted at daytime (between 7:30 and 22:00). Flight distance experiments were conducted opportunistically. Once a deer was detected, the observer walked towards the individual slowly (c. 0.5 m/s) and in a neutral way (no scaring or direct glaze) until the moment when the individual left its location. At this time, the observer stopped, and recorded the distance at which the deer flew (flight distance). We also recorded the distance at which the approach started (starting distance) as well as the date, the time, the habitat (coastal vs. interior forest – available only in 2012), the deer behavior at the beginning of the approach (i.e. standing or resting), the deer identity (from ear-tag or natural marks) and if the deer was alone or in presence of conspecifics (generally detectable within a 30m-radius).

Because experiments conducted on resting deer were rarer and because flight distances may differ between resting and standing deer (e.g. Grau & Grau 1980), we excluded from the analysis measurements done on resting deer. Similarly, to limit confounding factors (review in Stankowich 2008) we also excluded experiments when the deer was in presence of conspecifics.

We identified three temporal periods: the pre-hunt (before May 1), the hunt (from May 2 to May 25) and the posthunt (from May 26). To limit pseudo-replications, only the first measurement of a given individual that matched the above criteria was analyzed for each

habitat and temporal period during a given year. When a doubt occurred on the identity of unmarked deer we kept only a measurement per sex- and age- class (i.e. fawn, subadult and adult male and female) for each habitat and temporal period during a given year. This resulted in a subsample of 68 measurements conducted on a minimum of 18 individuals on East Limestone (13 marked deer and a minimum number of 6 unmarked deer) and a minimum of 13 individuals in the hunting area on Kunga (8 marked deer and a minimum of 5 unmarked deer) (Table CA.IV.5).

Table CA.IV.5: Sample size to study the effect of the hunting for fear experiment on deer flight distance. The number of individuals subjected to the experiment was provided for each temporal period (pre-hunt, hunt and post-hunt) in 2011 and 2012 (hunting year) for each area (East Limestone, the hunting area on Kunga) and each habitat (costal vs. interior forest for 2012 data). The number of marked/unmarked deer was provided under brackets.

Year : Area -habitat	Pre-hunt	Hunt	Post-hunt
2011: East Limestone		1 (1/0)	12 (8/4)
2012 : East Limestone – coastal Forest	7 (5/2)	1 (1/0)	9 (7/2)
2012 : East Limestone – interior Forest	2 (2/0)	3 (3/0)	6 (5/1)
2011: hunting area in Kunga		2 (1/1)	7 (5/2)
2012: hunting area in Kunga – coastal Forest	0	3 (3/0)	3 (3/0)
2012: hunting area in Kunga – interior Forest	4 (1/3)	1 (1/0)	7(4/3)

II.B. ANALYSIS

For each temporal period and year, each area (East Limestone vs. hunting area) and each habitat when available (coastal vs. interior in 2012) we calculated the average flight distance for marked and unmarked deer, separately. In addition, we studied the equivalent pattern for starting distance, to control for a possible bias due to the experimental conditions (Cooper 2008; Stankowich 2008; Dumont et al. 2012).

III. RESULTS & DISCUSSION

On East Limestone, flight distances ranged between 2 and 16 m, except for one measurement that reached 30 m in the coastal forest during the posthunt period in 2012 (Figure CA.IV.3 a). Flight distances were fairly similar between years and temporal period with a mean range of c. 4-9 m.

In the hunting area on Kunga, flight distances were more variable and ranged between 5 and 37 m but with >80% of values below 20 m (Figure CA.IV.3 b). Overall flight distances tended

to increase between the hunt and the posthunt period (Figure CA.IV.3 b), but so did the starting distance (Figure CA.IV.3 c). Thus, the present dataset did not allow exploring the effect of the hunting for fear on deer flight behavior, due to possible experimental biases.

Flight distances seemed to be variable on Kunga which may suggest that individuals may use different strategies in response to an approaching human. Indeed we noted that almost 50% of Kunga deer subjected to repeated flight distance experiments flew consistently at distances below 15 m (all were marked deer) whereas about 25% of Kunga deer (half marked and half unmarked) flew consistently at distances greater than 15 m. These proportions should be considered with caution as our analyses included only deer that were detected by humans, and hence did not account for individuals that would have detected humans first and left the area before we could conduct this experiment. However, this may suggest that flight distance may be linked to deer personality, with some deer more eager to stay whereas other would leave (Stankowich & Coss 2006). This may be an interesting perspective to explore to better assess how predator-naïve deer respond to risk in heavily browsed environment.

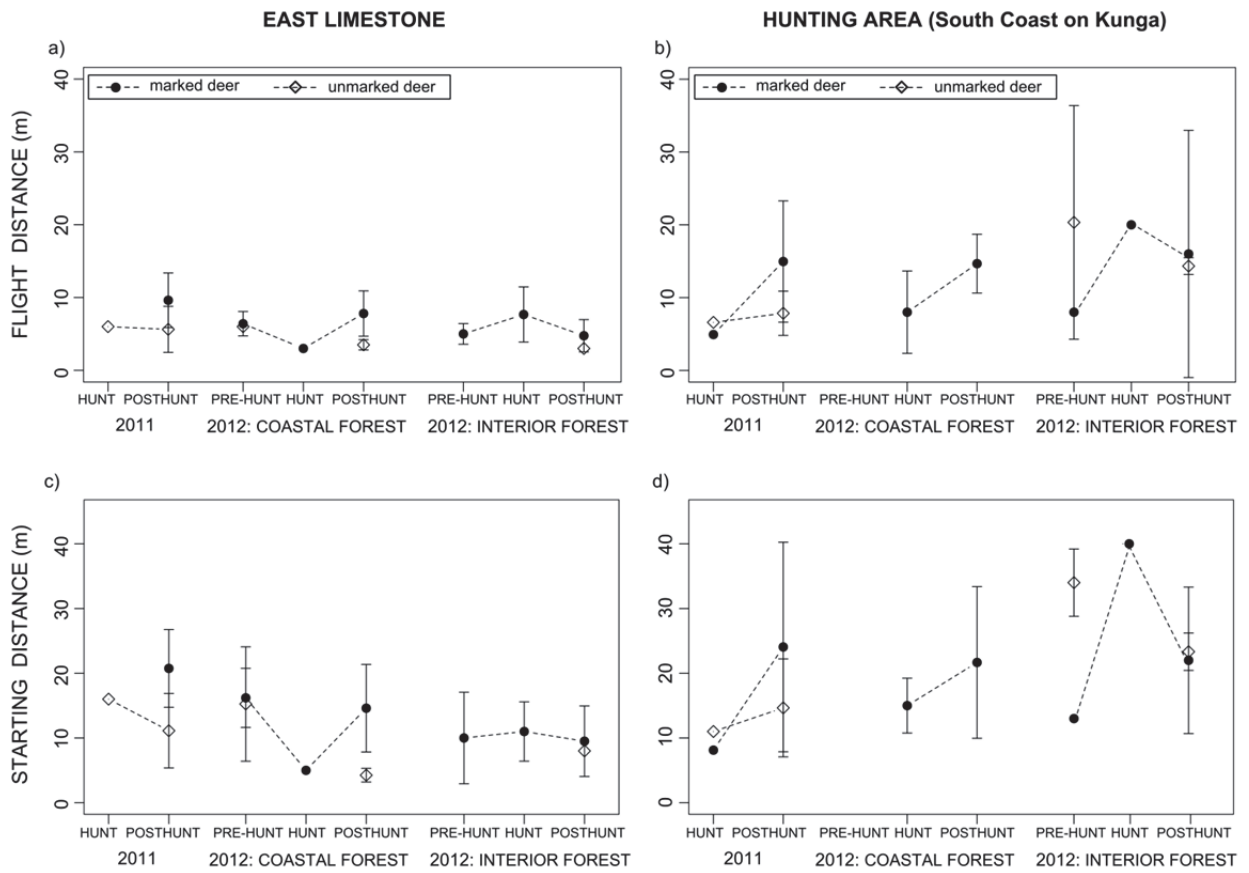


Figure CA.IV.3: Effect of the hunting for fear experiment on deer flight behavior on East Limestone (a,c) and in the hunting area on Kunga (b,d). Flight distances (mean \pm sd : a,b) of marked (closed dots) and unmarked deer (open dots) were provided for each year (2011 and 2012) and each temporal period (pre-hunt, hunt and posthunt). In 2012, coastal and interior habitats were analyzed separately. The equivalent representation is used for the average starting distances (mean \pm sd) (c,d).

CA.IV.D. DEER ACTIVITY PATTERN IN RESPONSE TO THE HUNTING FOR FEAR EXPERIMENT

Hunting and predation risk are largely recognized for their impact on deer activity pattern (e.g. Kilpatrick & Lima 1999; Cleveland et al. 2012; Bonnot et al. 2013). Thus, we explored if and how the hunting for fear experiment affected deer activity. We considered three activity indices: i) a diurnality index which compared deer activity levels at day- and night-time (Hoogenboom et al. 1984); ii) movement rate which is a common measure of deer activity (e.g. Beier & McCullough 1990; Boyce et al. 2010; Massé & Côté 2013); and iii) the degree of functional coupling (DFC) which informs on the level of synchrony between deer activity rhythm and the circadian cycle (Scheibe et al. 1999).

These indices could be computed only for collared deer and encompassed only a limited number of adult does (2011: 2 on East Limestone and 4 on Kunga, 2012: 7 on East Limestone and 3 on Kunga, Figure 11). We studied deer activity between April 1 and June 30 in 2011 and 2012. For all activity analyses we considered three temporal periods: the pre-hunt (April 1 to April 30), the hunt (May 2 to May 25) and the posthunt period (May 26 to June 30). In addition, for the diurnality index and movement rates we also identified hunted days from non-hunted days during the hunt period.

We studied the effect of the hunting for fear at the population (population of collared deer) and individual scale. At the population scale, we compared the temporal patterns in deer activity between the three control condition (East Limestone 2011, 2012 and Kunga 2011: Table CA.IV.1) and the treatment condition (Kunga 2012). At the individual scale, we compared the temporal pattern in the activity of three deer individuals for which activity data were available in April-June 2011 and 2012.

I. DIURNALITY INDEX

In response to diurnal hunting, deer may become more nocturnal (e.g. Kilgo et al. 1998; Kilpatrick & Lima 1999).

I.A. MATERIAL & METHODS

We investigated this aspect by using Hoogenboom et al.'s (1984) diurnality index (DI) (Equation CA.IV.1).

$$DI = \frac{A_{day} - A_{night}}{A_{day} + A_{night}} \text{ (Equation CA.IV.1)}$$

with A_{day} and A_{night} the proportion of time when deer was active at day- and night-time, respectively. This index ranges from -1 (strictly nocturnal) to 1 (strictly diurnal). For each collared doe, we used calibrated activity data (see Technical context A) to identify activity periods and computed daily DIs between April 1 and June 30 in 2011 and 2012. We explored several definitions of day- and night-time, excluding twilight periods ranging from 0 to 2 hour-periods around civil sunrise and sunset time. Results were similar for all day- and night-time definitions. Thus, here we presented the results assessed with the simplest definition of day- and night-time based on civil sunset and sunrise without twilight.

For each deer (individual scale) we calculated the average DI value for each temporal period (pre-hunt, non-hunted and hunted days during the hunt and posthunt). We then computed the average DI values for each conditions (population scale: East Limestone 2011, East Limestone 2012, Kunga 2011 and Kunga 2012; Table CA.IV.1) and compared their temporal trends.

I.B. RESULTS & DISCUSSION

At the population scale (Figure CA.IV.4 a,b), mean DI values ranged between 0.21 and 0.55. This indicated that during the study period (April-June), deer were more active at day (c. 40-50% of the time active) than at night-time (c. 20-25% of the time active). This is in agreement with previous study on deer activity budget and pattern during the spring (e.g. Belovsky & Slade 1986; Beier & McCullough 1990; Parker et al. 1999; Massé & Côté 2013).

On East Limestone, DI values decreased by 42% from April to June in 2011 and in 2012. Increasing proportion of activity during the night may be explained by seasonal changes in deer status (e.g. reproduction) and/or in environmental conditions (e.g. Anderson 1959; Montgomery 1963; Beier & McCullough 1990; Hayes & Krausman 1993). In particular, this may be explained by the presence of small groups of research volunteers in May-June on East Limestone. This hypothesis might be valid because no decrease in DIs was observed on Kunga in 2011 (Figure CA.IV.4 b). If validated this would support the fact that on East Limestone deer may be disturbed by volunteers' activities (Chapter III), and deer would then tend to limit their diurnal activity in volunteer's presence. This seems also supported by the

results assessed for deer East Limestone 06, for which DI values also decreased by > 40% over the study period for both years (Figure CA.IV.4 d).

On Kunga, DI values were fairly constant at the population scale (mean DI: 0.27 ± 0.03) between April and June in 2011 and 2012. We noted that, during the hunted days in 2012, DI values might be slightly reduced in comparison to other 2012 DI values as well as when compared to the pattern observed in 2011 when DIs might be increasing between the pre-hunt and the hunt periods. Whether this subtle contrast may be interpreted as a response of deer to the hunting for fear cannot be assessed here. This might be supported by the data assessed on deer K 05 (Figure CA.IV.4,d), which showed an increasing trend in DI values in 2011 against a decreasing trend in DI values in 2012. However, deer K 07 showed the opposite pattern, with a decreasing trend in 2011 and an increasing trend in 2012.

The hunting for fear experiment did thus not seem to have a strong impact on the periods of activity of collared deer, and if it had some this would be subtle changes requiring larger and finer dataset to be identified.

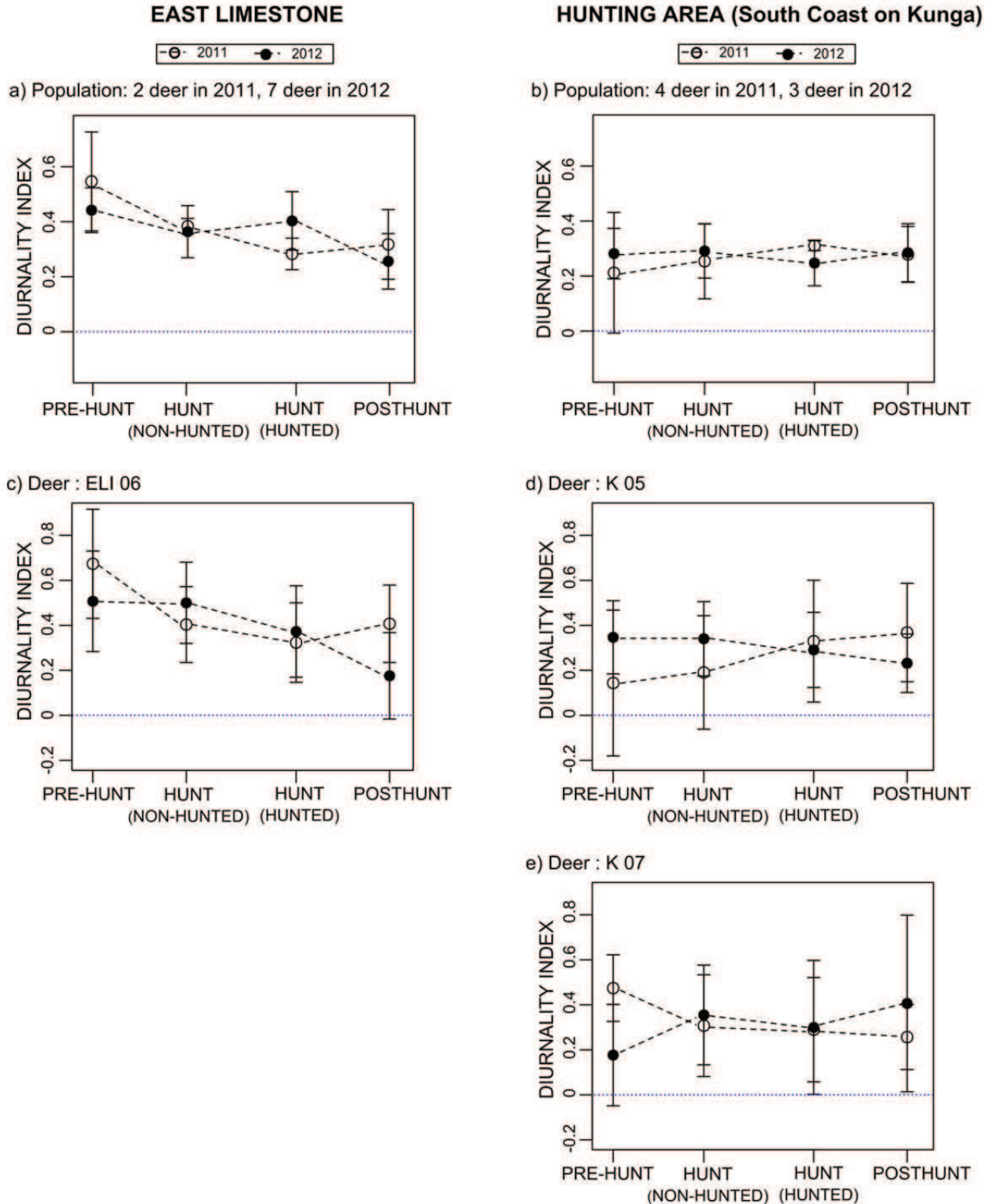


Figure CA.IV.4: Effect of the hunting for fear experiment on deer diurnality index. Diurnality index (DI : mean \pm sd) was presented in relation to the temporal period (pre-hunt, non-hunted and hunted days during the hunt and posthunt) in 2011 (open dots) and 2012 (closed dots – hunting year) on East Limestone (a,c) and in the hunting area on Kunga (b,d,e). DI was calculated at the population scale (a,b) and at the individual scale (c) and two individuals on Kunga (d, e). And equally level of diurnal and nocturnal activity is marked by the line at 0.

II. MOVEMENT RATE

In response to hunting, deer are expected to be more active (e.g. Cleveland et al. 2012) and this particularly during the less risky night-time (e.g. Kilgo et al. 1998). We explored this aspect by comparing deer movement rate at day and night-time, and expected deer to be more active at night-time during the hunt in the hunting area. This pattern could be exacerbated during the hunted days.

II.A. MATERIAL & METHODS

We used GPS locations recorded every 30-min between April 1 and June 30. We coupled GPS locations and calibrated activity data (see Technical context) to calculate the proportion of activity measurements during each step (i.e. between two locations). For this analysis, we considered that a step was active if this proportion was above 50% (hereafter conservative active step). For each of this conservative active step, we estimated the movement rate as the distance travelled during a given step.

For each deer (individual scale) we calculated their average movement rate at day and night-time for each temporal period (pre-hunt, non-hunted and hunted days during the hunt and post-hunt periods). We then computed the average movement rates at day- and night-time for each conditions (population scale: East Limestone 2011, East Limestone 2012, Kunga 2011 and Kunga 2012; Table CA.IV.1) and compared the temporal trend among them.

II.B. RESULTS & DISCUSSION

At the population scale, mean movement rates ranged between 1.3 and 2.8 m/min (equivalent to 80 – 168 m/h). This fell within the lower range of movement rates reported for mule and black-tailed deer (e.g. : mean range: c. 0.8 - 6 m/min : Eberhardt et al. 1984; c. 1.5 - 7 m/min Parker et al. 1996).

Overall, movement rates did not seem to be affected by the hunting for fear experiment. No peak in movement rates could be detected during the hunt in the hunting area and movement rate at night-time were similar to lower than those at day-time (Figure CA.IV.5). Note that during the non-hunted days, movement rate of deer K 07 was 1.5 times higher at night than at daytime during the hunting year (2012) (Figure CA.IV.5 e). However, variability was so high that this pattern may not be relevant.

The levels of variability among measurements at the individual scales were relatively high within a given temporal period and a given period of the day (day/night). Indeed standard errors were estimated to be between 40 and 60% of the mean value associated (Figure CA.IV.5 c,d,e). This seemed to support the effect of local conditions at finer scales on deer movement rates (e.g. weather conditions, habitat features: Belovsky & Slade 1986; Beier & McCullough 1990; Parker et al. 1999) and might emphasize the need to integrate environmental variables to study deer movement rate (e.g. Massé & Côté 2013).

To conclude, the hunting for fear experiment did not seem to affect collared deer movement rates.

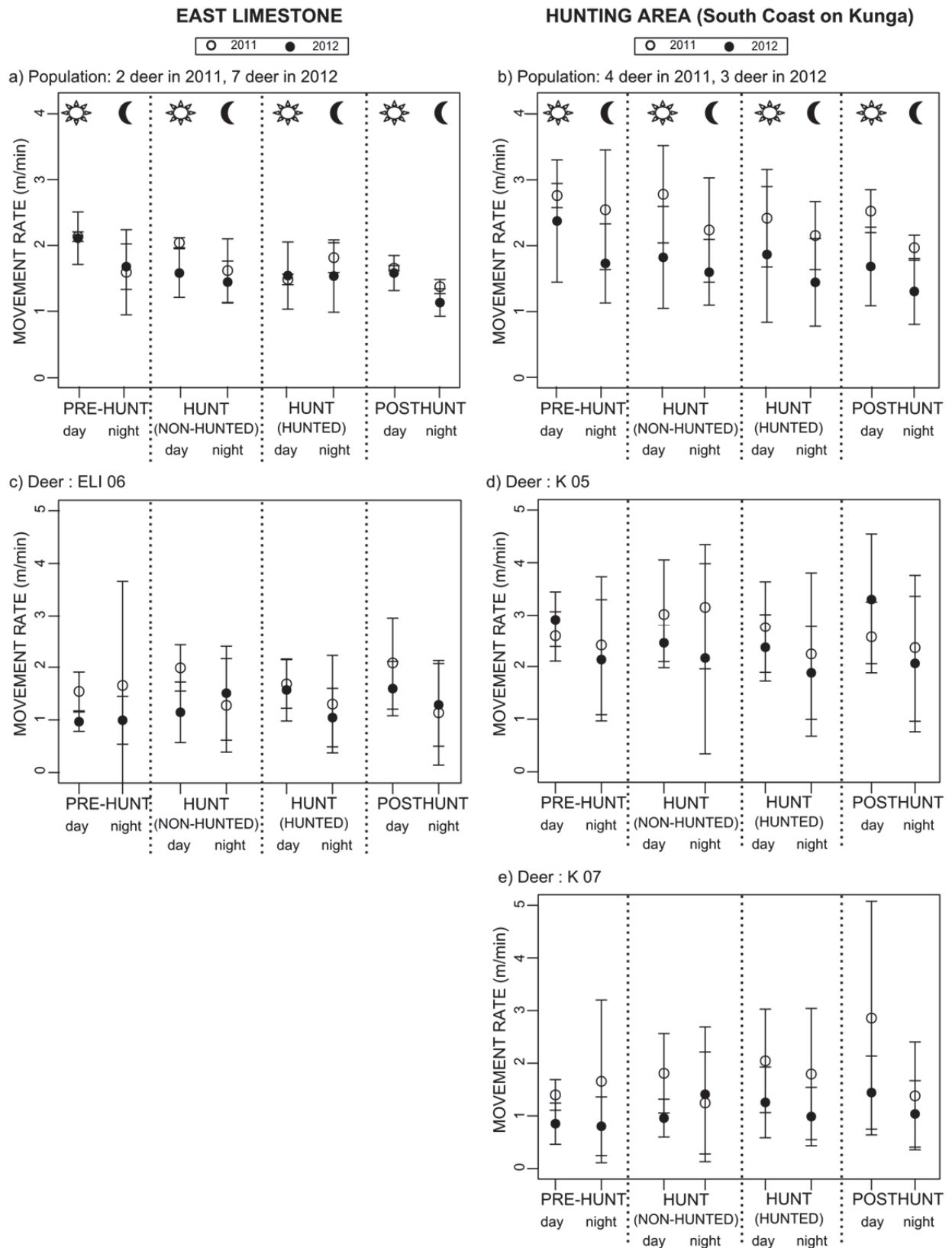


Figure CA.IV.5: Effect of the hunting for fear experiment on deer movement rate. Movement rate (mean \pm sd) was presented in relation to the temporal period (pre-hunt, non-hunted and hunted days during the hunt and post-hunt) at day (sun) and night-time (moon) in 2011 (open dots) and 2012 (closed dots – hunting year) on East Limestone (a,c) and in the hunting area on Kunga (b,d,e). Mean movement rate was calculated at the population scale (a,b) and at the individual scale for an individual on East Limestone (c) and two individuals on Kunga (d, e).

III. DEGREE OF FUNCTIONAL COUPLING: A MEASURE OF RHYTHM SYNCHRONY

III.A. BIOLOGICAL RHYTHMS AN INDICATOR OF ANIMAL CONDITION.

All animals face changing environmental conditions during their lifetime. Although stochastic environmental changes may occur, environments are generally characterized by periodic changes among years (e.g. El Nino), seasons (e.g. summer vs. winter), days or hours. In particular, environmental conditions (e.g. temperature, humidity, daylight) change over a day within a 24-h cycle, namely “circadian cycle” or “circadian rhythm”. In response, animals adjust their behavior to cope with the daily fluctuations in their environments as function of their needs and constraints (Scheibe et al. 1999; Berger et al. 2003).

Disturbances, such as stressful events, disease or discomfort, may affect animal biological rhythms, resulting in lower level of synchrony between the activity rhythms of an individual and the cyclic changes of its environment (e.g. Scheibe et al. 1999; Berger et al. 2003; review in Krop-Benesch et al. 2011). In particular, hunting was reported to affect activity rhythms of German Przewalski horses which presented lower synchrony levels with the circadian cycle during the hunt period (Scheibe et al. 1999).

We explored this aspect and investigated if the hunting for fear experiment affected deer activity rhythm by using the degree of functional coupling (DFC: Scheibe et al. 1999), as indicator of the level of synchrony between deer and the circadian cycle. We expected that DFC values would drop during the hunt in the hunting area on Kunga.

III.B. MATERIAL & METHODS

III.B.1. DEGREE OF FUNCTIONAL COUPLING: PRINCIPLE

The principle of the analyses is briefly summarized here but for further details on the mathematical background, see Krop-Benesch et al. 2011 and Riotte-Lambert et al. 2013. Time series, such as activity data over a given period, can be decomposed into a sum of oscillations characterized by their period and their intensity. Such decomposition is called Fourier transform. Period that are divisors of 24-hour (circadian period) are called harmonic periods. The contribution of each period to the original time series varies among periods and several mathematical tests exist to identify the periods which have a significant contribution to describe the original time series.

The Degree of functional coupling (DFC) consists in calculating the ratio between the cumulative intensity of significant harmonic periods and the cumulative intensity of all significant periods (Equation CA.IV.2). DFC informs thus on the relative contribution of harmonic periods among all periods that explain significantly the original time series. DFC ranges between 0 (total asynchrony between the individual activity rhythm and the circadian rhythm) and 1 (perfect synchrony between the individual activity rhythm and the circadian rhythm).

$$DFC = 100 \cdot \frac{\sum I_{\text{significant.harmonic.period}}}{\sum I_{\text{significant.period}}} \text{ (Equation CA.IV.2)}$$

With $I_{\text{significant.harmonic.period}}$ the intensity of a given significant harmonic period and $I_{\text{significant.period}}$ the intensity of a given significant period.

III.B.2. COMPUTATION AND ANALYSES

We used calibrated activity and coded inactivity by 0 and activity by 1 (see Technical reports). We calculated DFC in adapting Krop-Benesch et al.'s (2011) method to categorical data. We computed DFC for consecutive time series of 7-days with a 1-day shift and a 6-day overlap between successive dataset. For each 7-day dataset, we conducted Fourier transform and identified significant periods with a 5% type I error using Riotte-Lambert et al.'s (2013) procedure. Within these significant periods, we identified 24-hour divisors (harmonic periods) and computed DFC according to equation CA.IV.2.

We calculated DFC values between April 1 and June 30 in 2011 and 2012 for collared deer on East Limestone and on Kunga (individual scale). We then computed the average DFC value among individuals for each 7-day interval for deer on East Limestone in 2011 and 2012 and deer on Kunga in 2011 and 2012 (population scale, Table CA.IV.1) and compared their temporal trends.

III.C.RESULTS

Overall, the hunting for fear experiment did not seem to affect deer DFC. No drop in DFC could be detected during the hunt in the hunting area (Figure CA.IV.6). In particular, DFC remained constant at levels closed to 85% at both the population and individual scale on Kunga during the hunt (Figure CA.IV.6 b,d,e). In addition, at the population scale, both

islands presented similar DFC levels with mean values ranging between 72 and 93% (Figure CA.IV.6 a,b). These levels were similar to those observed in undisturbed red deer in Germany placed in enclosure (mean DFC \pm sd: 84 \pm 9%) or in semi-natural environments (DFC: 70 \pm 12%) and were higher than those observed in disturbed red deer (e.g. handling, chase) which presented DFC between 4 and 52% (Berger et al. 2003). Consequently, the activity rhythm of collared deer did not seem to be disturbed by the hunting for fear.

IV. SUMMARY OF THE EFFECT OF THE HUNTING FOR FEAR EXPERIMENT ON DEER ACTIVITY PATTERN

Overall the three activity indices suggested that the hunting for fear experiment did not have strong effect on the activity pattern of collared deer on Kunga. During the hunt, deer on Kunga did not seem to shift towards more nocturnal behaviors, they did not increase their movement rates and did not show a reduction in their level of synchrony with the circadian cycle. The hunt might have created subtle changes in deer activity periods (analysis CA.IV.A), however, finer and larger dataset are required to investigate this possibility. Interestingly, deer on East Limestone may have tended to become more nocturnal when volunteers activity occurred (analysis A), if validated, this would support the fact that volunteer activity may also disturb deer vigilance (Chapter III). Remarkably, although limited, the current analyses provided a first assessment on deer activity pattern in the study and seemed in agreement with previous study on deer movement rate and activity rhythms.

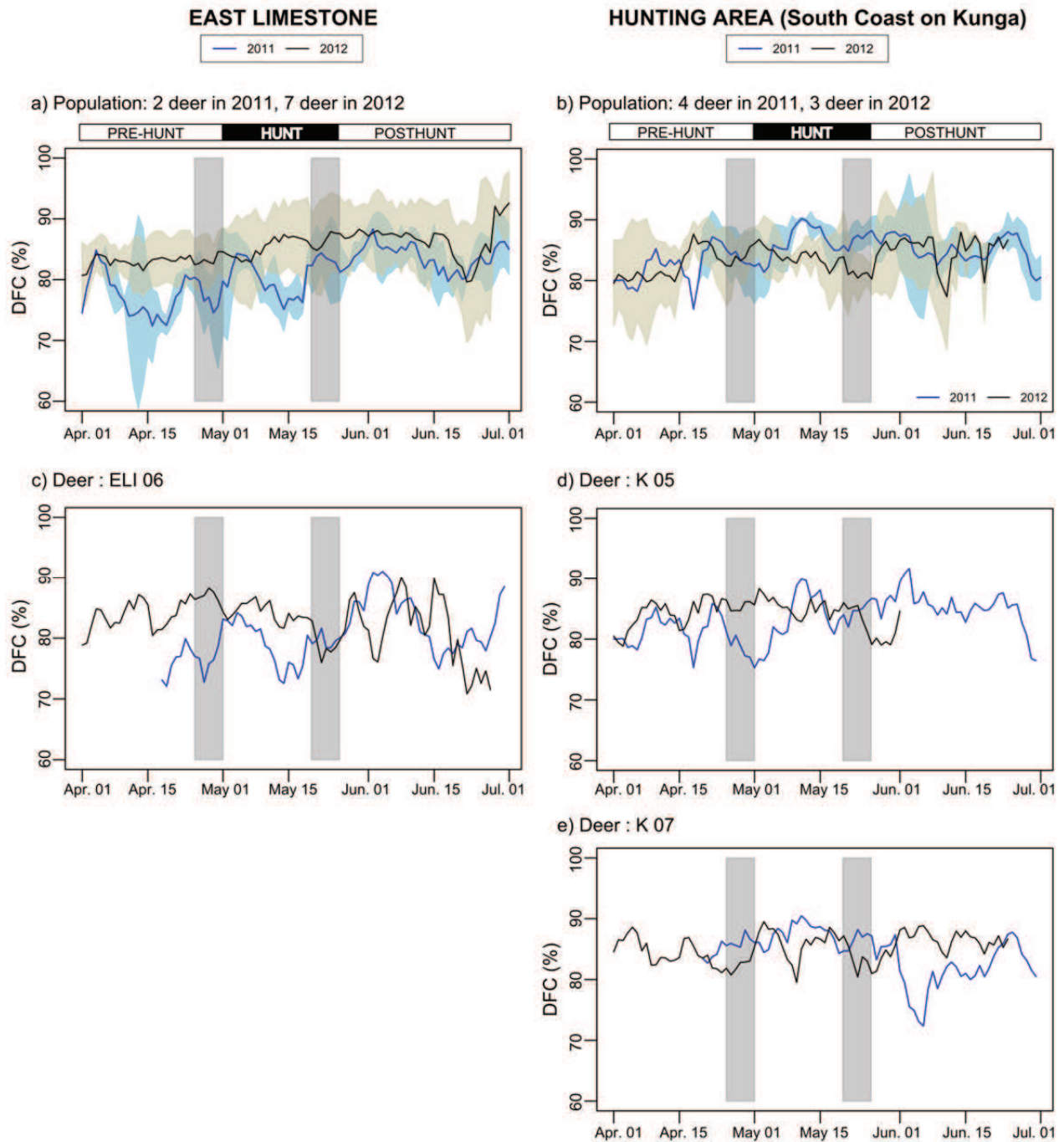


Figure CA.IV.6: Effect of the hunting for fear experiment on deer activity rhythms measured by the degree of functional coupling (DFC). DFC was calculated between April 1 and June 30 in 2011 (blue) and in 2012 (black) on East Limestone (a,c) and in the hunting area on Kunga (b ,d, e). The first day of the 7-day period considered to calculate DFC values was chosen as reference day to plot DFC value (i.e. DFC values plotted for April 15 was calculated on the period between April 15 and April 21). At the population scale (a,b), the solid lines marked the mean DFC value and the colored area around the mean line marked the standard deviations (blue for 2011 and cream for 2012). At the individual scale (c,d,e) solid lines marked the values assessed for each 7-day period. Grey zones identify 7-day period which included days in two different temporal periods (pre-hunt and hunt or hunt and posthunt). Lines stopped when no data were available.

CA.IV.E. DEER HABITAT USE IN RESPONSE TO THE HUNTING FOR FEAR EXPERIMENT

I. PREDICTIONS

During the hunt, deer are expected to avoid the hunting area (e.g. Vercauteren & Hygnstrom 1998; Millspaugh et al. 2000). However, spatial alternatives may not necessarily offer similar habitat to the risky area and animals may have to trade-off their time between risky and safe areas (Lima & Dill 1990). Deer should thus seek refuges in safe areas to rest and limit their use of the risky area to active foraging. We explored this aspect in studying deer habitat use in response to the hunting for fear experiment. We predicted that deer should avoid the hunting area as well as the intertidal zone where deer should perceive more risky due to the absence of cover. Deer may seek refuge in the safe and covered windfall areas. This response should be exacerbated in resting deer.

II. MATERIAL & METHODS

We considered three temporal periods: pre-hunt (April 1 to 30), hunt (May 1 to 25) and posthunt period (May 26 to June 30). For each deer and each temporal period, we calculated its utilization distribution (UD) when resting (resting UD) or active (active UD) (see Technical context). We then calculated for each UD the proportion of the given UD that fell in the hunting, intertidal and windfall areas. This provided the frequency of use of each zone.

The hunting area was defined as the 100-m buffer from the shoreline in the South coast of Kunga (Chapter IV, Figure IV.1). Intertidal and windfall areas were defined according to the systematic mapping conducted on East Limestone and Kunga at a 50 x 50 m² scale (Introduction, Box 5). All analyses were conducted with ArcGis x9.3 and the R software (R Core Team 2012), with the *rgdal*, *raster* and *proj4* packages (Urbanek 2012; Hijmans 2013; Keitt et al. 2013).

III. RESULTS & DISCUSSION

Resting UDs were estimated to be between 10 and 25 ha and were similar between islands, with an average value estimated at 16 ± 4 ha on East Limestone and at 17 ± 4 ha on Kunga. Active UDs were estimated to be between 10 and 55 ha and were also similar between islands with average values estimated at 25 ± 7 ha on East Limestone and at 28 ± 10 ha.

Deer did not seem to avoid the hunting area during the hunting for fear experiment (Figure CA.IV.7). During the hunting year (2012), the frequency of use of the hunting area remained fairly constant between the pre-hunt and the posthunt period for both resting (27 ± 14%) and active deer (35 ± 16%). These frequencies were lower than in 2011 but this pattern was not consistent at the individual scale and might result from sampling artifacts.

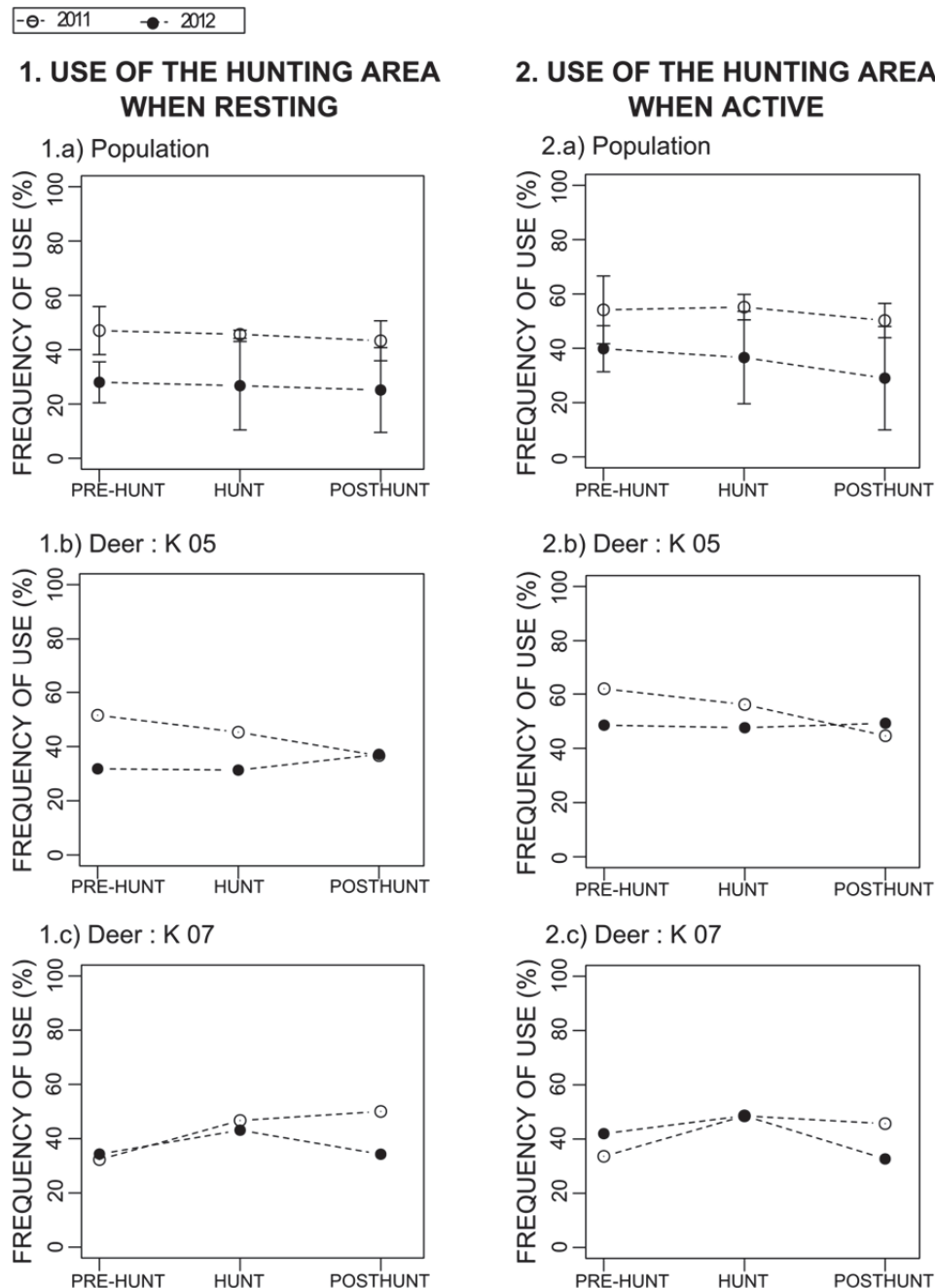


Figure CA.IV.7: Effect of the hunting for fear experiment on the frequency of use of the hunting area when deer are resting (1) or active (2). The frequency of use for resting and active deer was presented as function of the temporal period (pre-hunt, hunt, post-hunt) at the population scale estimated on 4 deer in 2011 and 3 deer in 2012 (a) and at the individual scale for two deer (b,c). Open dots marked data from 2011 and closed dots marked data from 2012 (hunting year).

The hunting for fear experiment did not seem to affect deer use of the intertidal areas (Figure CA.IV.8). Resting deer barely used the hunting area independently from the hunting for fear experiment and from the island (average frequency of use between 8 and 12%, Figure CA.IV.8 1). On Kunga, active deer did not decrease their use of the intertidal areas during the hunt in 2012 and maintained similar levels between the pre-and the posthunt in 2011 (c. 10-15%, Figure CA.IV.8 2).

Note that the decline in the frequency of use of the intertidal area in 2011 on both islands may be a sampling artifact but may also suggest that from April to June deer are more likely to use the growing terrestrial plants as food resource. In the latter case the absence of declining trend in 2012 might be explained by annual differences in vegetation growth, however, this should be confirmed.

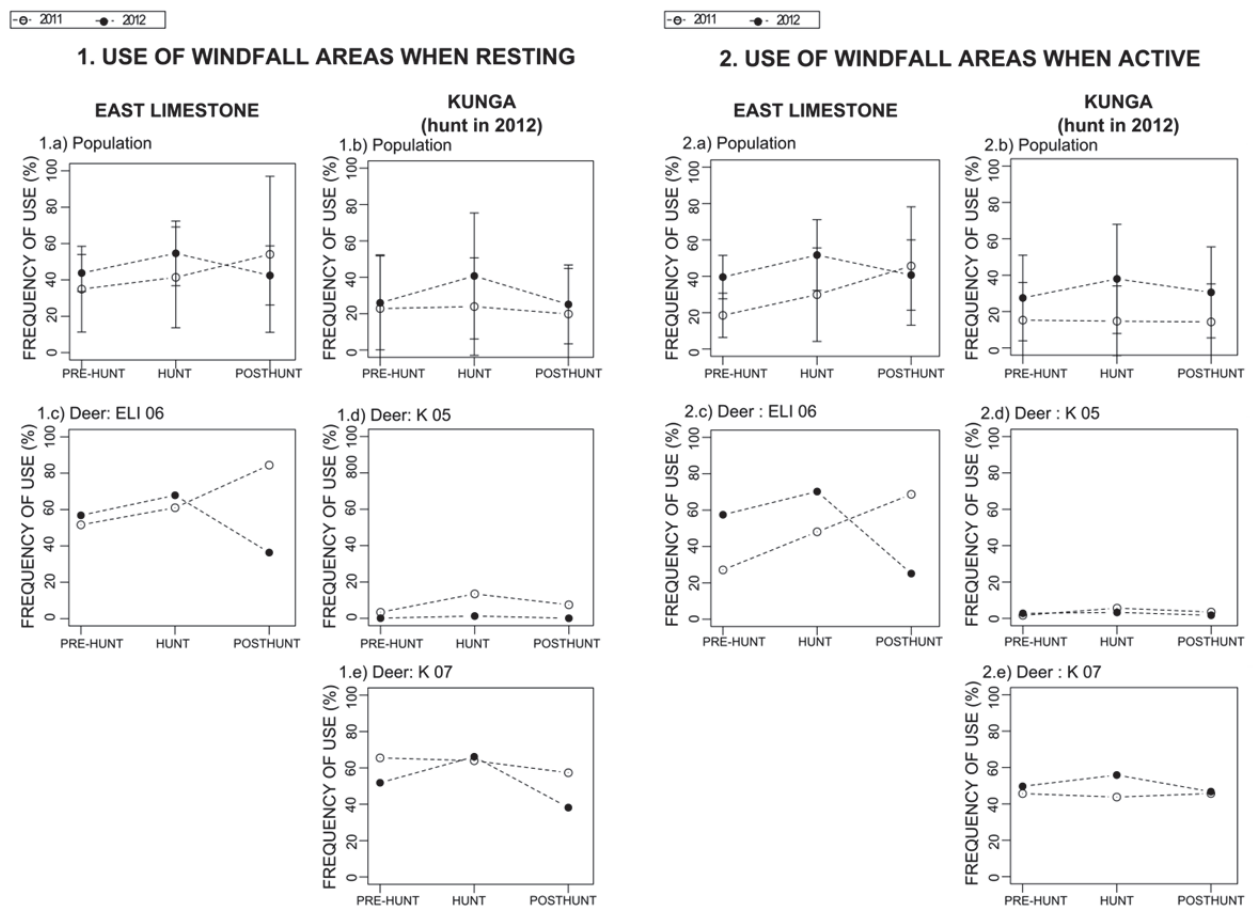


Figure CA.IV.8: Effect of the hunting for fear experiment on the frequency of use of the intertidal area when deer are resting (1) or active (2). The frequency of use for resting and active deer on East Limestone (a,c) and in the hunting area on Kunga (b,d,e) was presented as function of the temporal period (pre-hunt, hunt, post-hunt) at the population scale estimated on 2 and 7 deer in 2011 and 2012 on East Limestone (a) and estimated on 4 and 3 deer in 2011 and 2012 on Kunga (b), and at the individual scale for a deer on East Limestone (c) and two deer on Kunga (d,e). Open dots marked data from 2011 and closed dots marked data from 2012 (hunting year).

The effect of the hunting for fear experiment on deer use of the windfall areas was inconclusive (Figure CA.IV.9). As expected the frequency of use of the windfall areas by resting and active deer increased during the hunt in 2012 (Figure CA.IV.9 1b,2b). However, this pattern was also observed on East Limestone where no hunt occurred (Figure CA.IV.9 1a,2a). This suggested that seasonal effects may interact with the observed pattern and prevented from concluding on an effect of the hunting for fear on deer use of windfall area.

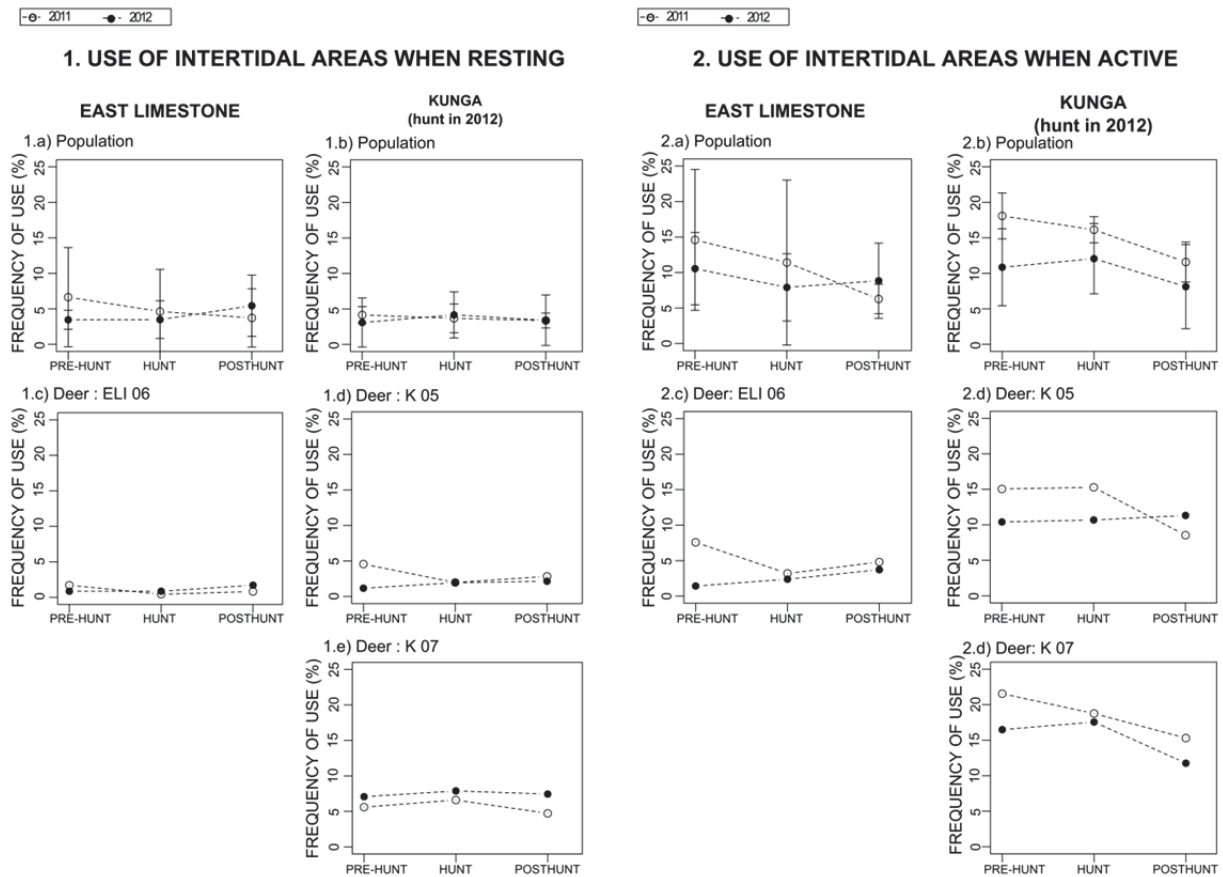


Figure CA.IV.9: Effect of the hunting for fear experiment on the frequency of use of windfall areas when deer are resting (1) or active (2). The frequency of use for resting and active deer on East Limestone (a,c) and in the hunting area on Kunga (b,d,e) was presented as function of the temporal period (pre-hunt, hunt, posthunt) at the population scale estimated on 2 and 7 deer in 2011 and 2012 on East Limestone (a) and estimated on 4 and 3 deer in 2011 and 2012 on Kunga (b), and at the individual scale for a deer on East Limestone (c) and two deer on Kunga (d,e). Open dots marked data from 2011 and closed dots marked data from 2012 (hunting year).

To conclude, the hunting for fear experiment did not seem to have affected the way collared deer on Kunga used their habitat, at least based on the coarse analyses presented here which considered only a broad scale. These preliminary analyses tend to support the fact that collared deer, as a subsample of marked deer, did not seem to avoid the hunting area or to change their habitat use at a the broad scale considered. Finer spatial analyses may

complement these analyses and inform on deer spatial strategies at finer scales, and may help to better assess the hunting efforts required to displace, significantly, resident deer from a given area and if such a displacement is feasible or not according to deer personality.

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TECHNICAL CONTEXT : DEER SPATIO-TEMPORAL BEHAVIOR ASSESSED BY ACTIVITY AND GPS-LOCATION DATA

GPS collars are equipped with activity sensors which records acceleration along two axes: the X-axis measures acceleration in forward/backward motions and the Y-axis measures acceleration in left/right motions. The activity sensor measures acceleration on both axes four times per seconds and records the cumulated measurements over a 4-minute interval. Acceleration values are stored as numeric values within a relative range between 0 and 255 on each axis. Because animals may move their head even when they are resting, a calibration is necessary if one wants to infer animal behaviors from these activity measurements. In other words, we need to identify numerical thresholds which allow classifying numerical activity data into biological classes of deer behaviors. We conducted this calibration by comparing direct observation data with recorded activity data.

A. CALIBRATION OF ACTIVITY DATA

A.1. Observation data

Between May 14 and June 21, 2011, I observed five free-ranging collared does (two on East Limestone and three on Kunga) at daytime (i.e. between 7:30 and 19:30). I located deer via the VHF signal emitted by their GPS collar and observed them at a mean distance of c. 10-20 m considered close enough to identify animal behavior and far enough to avoid disturbing its behavior. I identified five behaviors: feeding (i.e. standing or walking, consuming or looking for food without food intake for at least 2s); travelling (i.e. any abrupt movement (e.g. jumping a root) or slow travel without food intake for at least 2s); standing (i.e. remaining at one place without food intake, generally scanning); grooming and lying. Transition times between behaviors were recorded by hand according to a satellite-synchronized clock. Deer observations aimed at recording a maximum number of bouts for each behavior, with an emphasis with resting and feeding (Figure CA.IV.10). On average observation session lasted an hour with a median duration of c. 30 minutes. This resulted in 21.2 hours of deer observation with an average of 4.2 hours per individual.

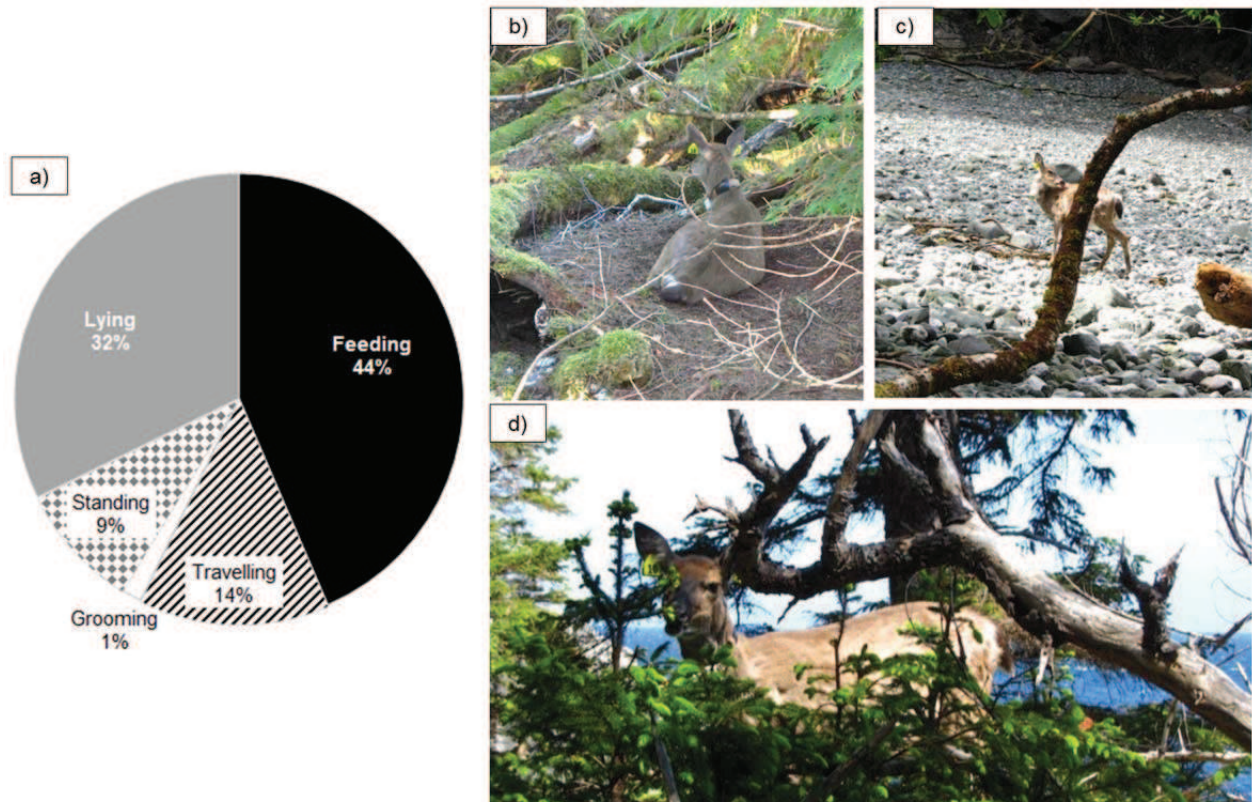


Figure CA.IV.10: Direct deer observations to calibrate activity data. (a) Total proportion of time spent in each behavior over 21.2 hours of observation on two and three collared does on East Limestone and Kunga, respectively, in May and June 2011. Examples of deer (b) lying, (c) grooming and (d) feeding on spruce as observed on East Limestone.

A.2. Analyses

To calibrate activity data, we discretized observation data in 4-min sequences (the same temporal interval as activity measurements). We excluded incomplete 4-min sequences (e.g. initial or final 4-min sequences). This resulted in 235 4-min sequences. For each of these 4-min sequences we calculated the proportion of time spent by the individual in each behavior (i.e. feeding, travelling, grooming, standing and lying). Because observation data were limited and two axes were insufficient to identify each behavior individually we reclassified deer behavior in two broader classes: Active and Inactive. The Active class pooled feeding, travelling and grooming behaviors, whereas the Inactive class pooled lying and standing behaviors. Lying and standing behaviors were pooled because deer rarely moved its neck when scanning and hence could not be distinguished from lying behavior via acceleration measurements.

For each 4-min sequence we calculated the proportion of time spent in Activity and Inactivity. A 4-min sequence was considered Active and Inactive, respectively, only when the proportion of time spent Active and Inactive was 100%. All other 4-min sequences were excluded from the analysis. This resulted in 142 4-min sequences. Among them, standing behavior accounted only for 6% of the time spent Inactive (lying accounting for the remaining 94%) and was thus a very good proxy for lying behavior (resting deer). In comparison, the Active class was more heterogeneous and feeding, travelling and grooming accounted for 65, 30 and 5% of the time spent active.

For each of these sequences, we used the sum of acceleration values recorded on both axes (X- and Y- axis) as activity measurement. We identified two numerical thresholds: i) a conservative threshold for inactivity and ii) a relevant threshold for activity. The former was used in any analyses considering resting deer, and particularly to measure the measurement error in GPS locations (in situ GPS noise). The latter was used in any analyses considering foraging deer.

Conservative threshold for inactivity

We identified the conservative threshold for inactivity as the minimum numerical value recorded for active 4-min sequence. All activity measurements below this threshold were classified as Inactive. This conservative threshold was estimated to be 18 (Figure CA.IV.12). We validated *a posteriori* the use of 18 as conservative threshold for inactivity in classifying all 4-min sequences with deer observations (i.e. including those excluded from the previous analysis because the proportions of Activity and Inactivity were not equal to 0 or 100%). For each of these 235 4-min sequences we calculated the average proportion of time deer spent in each behavior. When classified as Inactive, deer spent 93% of their time lying and spent less than 3% foraging or moving (Figure CA.IV.13).

Relevant threshold for activity

For the relevant threshold for activity, we used the Receiver Operating Characteristic (ROC) curve analysis (Metz 1978; Zweig & Campbell 1993). This analysis is based on the notion of true and false positives and negatives. If we arbitrarily decide that our goal is to detect the Active state, an observation we correctly classified as Active is a true positive. Symmetrically,

an observation we correctly classified as Inactive is a true negative. Conversely, observations which are misclassified as Active or Inactive are false positives or false negatives, respectively. Sensitivity is the proportion of true positives within the observations considered as positive (i.e. true and false positive), and specificity is the proportion of true negatives within the observations classified as negative (i.e. true and false negative; Figure CA.IV.11). Specificity and sensitivity depend on the threshold value. The higher the threshold is and the less errors in identifying positive values and the more errors in identifying negative values. Sensitivity increases and specificity decreases with increasing threshold values. By comparing specificity and sensitivity over the range of possible threshold values, optimal threshold values can be assessed. This comparison is possible with a ROC curve (Figure CA.IV.11). In addition, by comparing the ROC curve with a random classification, we can assess the performance of the numerical index used to discriminate positive from negative values. This is done in comparing the area under the ROC curve (AUC) with the area under the random line (Figure CA.IV.11). High values of AUC (i.e. close to 1) indicate a relevant index whereas low values of AUC (close to 0.5) indicate that this index does not perform better than a random classification. Once the index considered is validated (i.e. high AUC value) we can identify the optimal threshold value.

Various optimality methods exist and their selection depends on the relative importance one carries to specificity and sensitivity (Freeman & Men 2008). We considered two methods to identify the optimal threshold value: 1) the threshold that equalizes sensitivity and sensibility and 2) the threshold that maximized the percent of correctly classified observations (i.e. maximum of true positive and negative). We identified both optimal threshold values for each deer individually and for all deer pooled together in a single dataset. For two deer the data available were too limited to conduct a ROC curve analysis individually, thus ROC curve analyses were conducted on three deer individually and on a dataset pooling the five deer observed. This resulted in eight ROC curve analyses (four ROC curve analyses per method). All analyses were conducted with the R software (R Core Team 2012) and the *MASS* and *PresenceAbsence* packages (Venables & Ripley 2002; Freeman & Moisen 2008).

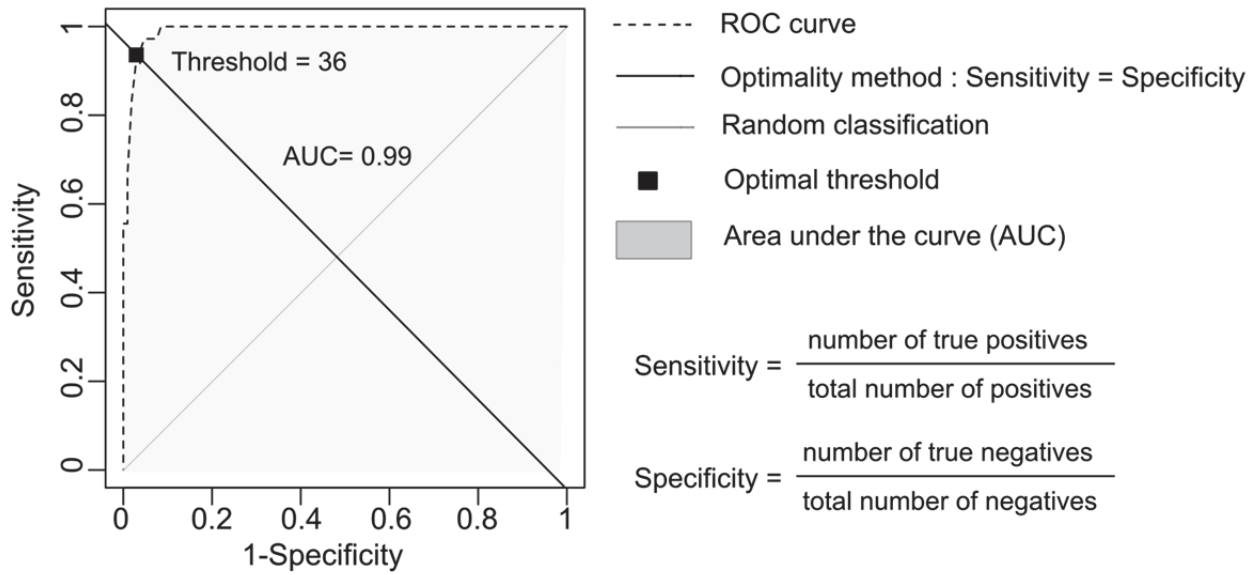


Figure CA.IV.11: Example of ROC curve analysis conducted on the dataset pooling the five deer together. The Receiver Operating Characteristic (ROC) curve is marked in dashed line. The grey line marks the random classification. The ROC curve has an area under the curve (AUC) estimated to be 0.99 (close to the maximum value of 1), indicating that using the sum of activity measurement on x- and y-axes is a relevant index to identify activity from inactivity. The optimality method used (sensitivity = specificity) is marked by the solid line. This enables to identify an optimal threshold for a value of 36 (intersection between the optimality method line and the ROC curve).

In our analyses, possible threshold values ranged between 0 and 256 and both optimality methods provided similar results with optimal threshold values ranging between 36 and 43 (Table CA.IV.5). In 88% of the analyses the optimal threshold value was between 36 and 38. We arbitrarily decided to use 36 as threshold value (Table CA.IV.5, Figure CA.IV.12).

Table CA.IV.6: Optimal threshold values assessed by ROC curve analyses on three deer individually (East Limestone 06, K 03, K 05) and on five deer pooled in a single analysis according to two optimality methods: method 1 equalizes sensitivity and specificity and method 2 maximizes the percent of observations correctly classified. Possible threshold values ranged between 0 and 256 in our analyses. Note that theoretically the sum of X-axes and Y-axes could reach 510 (2x255), however, among the 4-min sequences analyzed the maximum values recorded was 256.

Optimality Method	East Limestone 06	K 03	K 05	Five deer
Method 1: sensitivity = specificity	43	38	37	36
Method 2: maximum true positives and negatives	36	38	37	36

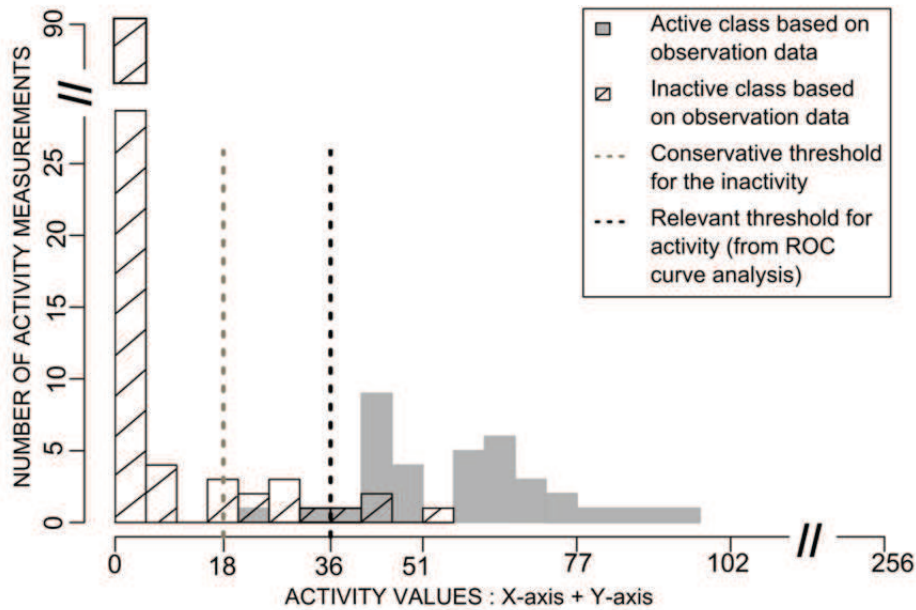


Figure CA.IV.12: Histogram of activity measurements (number of activity measurements in relation to their numerical values) identified by their activity class (active vs. inactive) assessed via observation data (grey: active class; hatched: inactive class). The grey dashed line marks the conservative threshold for inactivity (value = 18), below which no active data are recorded. The black dashed line marks the relevant threshold for activity assessed by ROC curve analysis (value = 36).

As previously, we validated *a posteriori* the use of 36 as optimal threshold for activity in classifying all 4-min sequences with deer observations according to this threshold. When classified as active, deer spent 85% of their time foraging or moving and less than 2% lying. When classified as inactive, deer spent 82% of their time lying and 15% of their time foraging or moving (Figure CA.IV.13). This validated the use of 36 as a threshold to identify active deer.

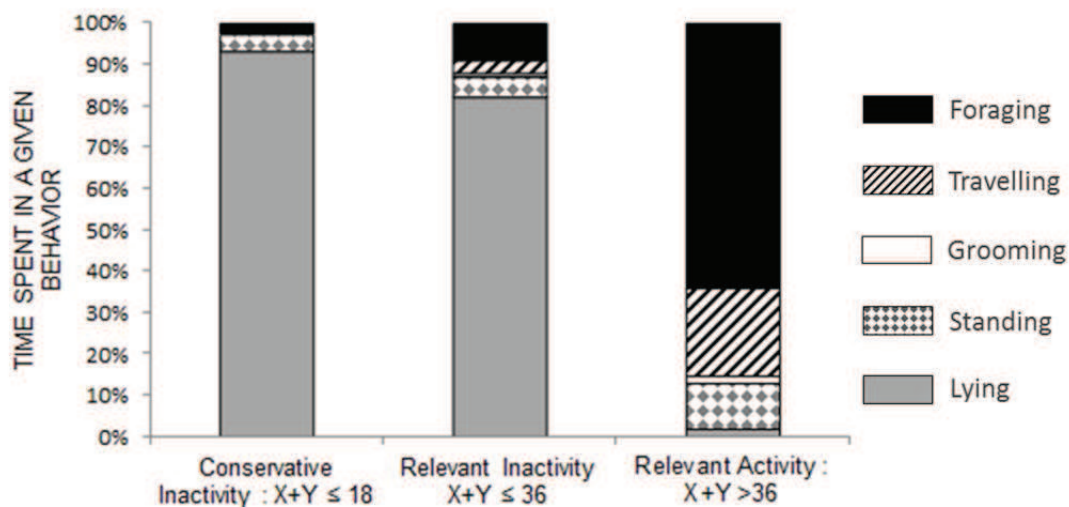


Figure CA.IV.13: Average proportions of time spent in each behavior (feeding, travelling, grooming, standing, lying) during 4-min sequences classified as inactive with the conservative threshold for inactivity (X+Y-axis values ≤ 18), and classified as inactive and active with the relevant threshold for inactivity assessed by ROC curve analyses (i.e. inactive class: X+Y-axis values ≤ 36 ; active class X+Y-axis values > 36).

In all analyses involving activity data (diurnality index, movement rate, degree of functional coupling, habitat use, CA.IV) we used the relevant threshold for activity (36) to identify active sequence and used the conservative threshold for inactivity (18) to identify resting sequences.

B. GPS LOCATIONS AND HOME RANGE ESTIMATION

B.1. Data management

In the present document, we considered only GPS locations acquired every 30 minutes. Locations acquired every four or five minutes during a few days in May and June 2011 and 2012 (Study system, Figure 10) were subsampled at 30-min interval. We excluded locations acquired by three or more satellites (3-dimensional locations) when their index of dilution of precision (DOP) was larger than 15 and, also excluded locations acquired by two satellites (2-dimensional locations) with DOP larger than 5 (Janeau et al. 2004). Furthermore, locations leading to a local speed larger than 50 m/min or to sharp V patterns with two legs longer than 200 m and an inner angle smaller than 25° were also excluded as they likely were artifacts (Figure CA.IV.14).

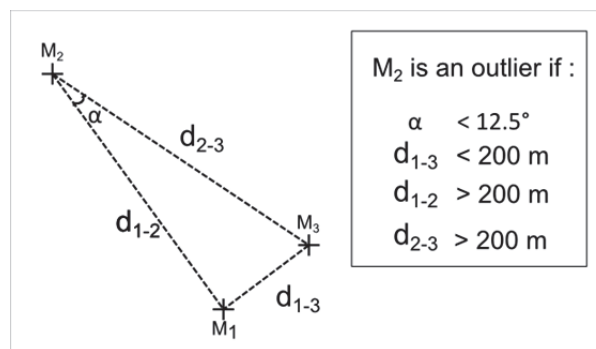


Figure CA.IV.14: Identification of location artifacts presenting a sharp V pattern. Considering three consecutive GPS locations M_1, M_2 and M_3 , M_2 is identified as an outlier if the angle α between M_1, M_2 and M_3 was smaller than 12.5° , the distance M_1-M_3 below 200 m and the distances between M_1-M_2 , and M_2-M_3 were greater than 200 m.

We then coupled GPS locations with calibrated activity data. For each step (couple of two consecutive locations) we calculated the proportion of active and inactive measurements according to the conservative threshold for inactivity and the relevant threshold for activity. Steps associated with conservative inactivity only (100% activity measurements fell below

the conservative threshold for inactivity equal to 18) were considered as “resting steps” and were used to assess the in-situ measurement error in GPS (see below). The terminal location of a resting step was considered as a resting location. We used resting locations to study how resting deer used their habitat. Steps associated with at least an activity measurement above the relevant threshold for activity (36) were considered as (partly) active and were included in the analyses of habitat use by active deer in proportion of their activity level.

Measurement error in GPS locations

To estimate in-situ measurement error in GPS locations (hereafter GPS noise) we calculated for each resting step the distance apparently travelled. We conducted this analysis on the 19 GPS collars set on adult females on East Limestone and Kunga between 2011 and 2012 (Study system, Figure 10). Over these 19 collars, we estimated the average GPS noise to be 21 ± 4 m (mean \pm sd), with an average median value of 16 ± 3 m.

Habitat use and home range computation

Habitats can be defined at various spatio-temporal scales according to the resources required by and available to deer and a large body of science has been focusing on how deer use their environment (e.g. Chang et al. 1995; Boroski et al. 1996; Boyce et al. 2003; Frair et al. 2005; Barja & Rosellini 2008; Fryxell et al. 2008; Bjørneraas et al. 2011; Singh et al. 2012; Bonnot et al. 2013). Given the data available, in the present study we investigated deer habitat use within deer home range (see below) and considered only three habitats (forest, windfall and intertidal areas, see Introduction, Box 5).

Home range refers to the spatial stable area used by an individual over a given period of time (Burt 1943; Krausman 1999; revisited by Powell 2000; Van Moorter 2008). A related concept is the “Utilization distribution” (UD: Van Winkle 1975) which associates to the extent of the area used by an individual the intensity of use of this area. Note that the intensity of use is linked to the animal’s familiarity with its environment (Powell 2000). Many estimators have been developed to assess animals’ UDs (e.g. review in Worton 1987; Seaman & Powell 1996; Powell 2000; Nathan et al. 2008; Kie et al. 2010; Walter et al. 2011). Because, resting and active animal are likely to select different resources (Frair et al. 2005; Godvik et al. 2009), we considered two kinds of UDs : i) “resting UD” for resting deer based

on resting locations; and ii) “active UD” for active deer based on active steps. We computed resting and active UDs, respectively, with location-based (Worton 1989) and movement-based (Benhamou 2011) kernel density estimation (KDE).

In both cases, inaccessible areas (seas) were taken into account through virtual barriers which were included in the KDE (Benhamou & Cornélis 2010). The goal is to prevent the UD to overflow into unsuitable (never or negligibly visited) habitats. We defined a barrier around East Limestone and Kunga at c. 50-100 m from the island border defined as the sea level. The border was refined using both GPS locations and expert knowledge on areas useable by deer. In addition, a 50-100-m band around the island enabled to account for deer using the intertidal area without overestimating the time spent in the sea (Figure CA.IV.15 and CA.IV.16).

GPS collars provide clouds of locations. The area including all locations can be discretized in spatial units (pixels or quadrats) using a virtual grid. The frequency of use of each quadrat can then be estimated (i.e. the density of locations in each quadrat). This provides a spatial histogram of the intensity of use (or utilization) of each quadrat. The KDE makes it possible to smooth such a discrete histogram into a continuous distribution, so as to get rid of arbitrary choices in terms of grid origin and pixel size. Because distribution tails are usually poorly estimated, the UD is generally estimated up to a cumulative probability of 0.95 and home range are generally defined as the total area encompassed within this 0.95 isopleth.

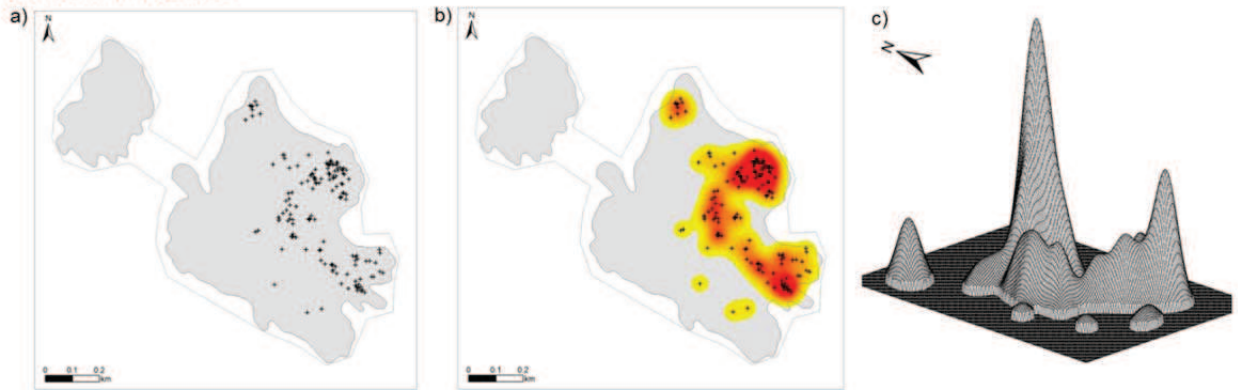
A critical stage in the use of KDE is the choice of the “smoothing parameter” (also referred to as “bandwidth”) which should be set to a value that balances over- and undersmoothing. The higher the smoothing parameter and the more flattened the distribution is, what tends to wash out actual differences in densities. Conversely, the lower the smoothing parameter and the more scattered the distribution is, what highlights irrelevant differences in densities due to sampling noise. In location-based KDE, there are a number of techniques that have been developed to determine the “best” smoothing parameters (e.g. Worton 1987, 1989; Seaman & Powell 1996). However, they do not seem to provide suitable results for auto-correlated locations (Benhamou 2011). In movement-based KDE, the density is computed from active time between successive relocations (step) rather than from locations themselves. In this case the determination of the smoothing parameter is simpler as it is

related to the degree of diffusion of the animal's movement and to the degree of uncertainty about the animal's location at intermediate times (i.e. between recorded locations). Note that the degree of uncertainty is maximum at mid-time between recorded locations and minimum for recorded locations, where it depends, at least partially, on the GPS noise (Bullard 1999). Another important point to note in the use of movement-based KDE is that the actual movement has to be assumed to be homogeneous between any two successive relocations, although it is free to change between movement steps.

In the present study, for movement-based KDE (to compute "active UD"), we used a minimum smoothing parameter equal to 30 m (i.e. slightly larger than the GPS noise, estimated to be c. 20 m). We used a diffusion coefficient equal to 100 m²/min, 100 being the order of magnitude of diffusion coefficients estimated for each GPS collars individually (range c. 70-130 m²/min). We fixed the maximum time span during which one can warrant that the movement is likely to be homogenous to be 60 minutes. For further details on the parameter definitions and the method used, see Benhamou (2011). For consistency, we used a smoothing parameter equal to 30 m in location-based KDE (to compute "resting UD").

All UD were computed with BRB/MKDE software which can be freely downloaded from www.cefe.cnrs.fr/ecologie-comportementale/simon-benhamou. Distances were measured via UTM9N projection system and the datum WGS 84. These analyses were conducted only for data acquired between April and June in 2011 and in 2012 to study the effect of the hunting for fear experiment (Chapter IV).

Deer ELI 06 in May 2011



Deer K 07 in May 2011

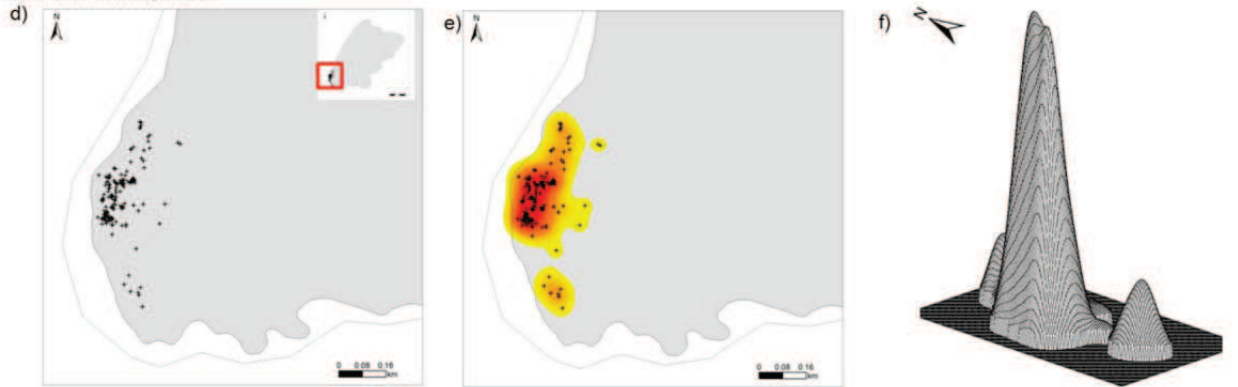


Figure CA.IV.15: Examples of resting utilization distribution (resting UD) computed with location-based kernel density estimation (KDE) for a deer on East Limestone (a,b,c) and on Kunga (d,e,f). (a, d) show resting locations identified as the terminal locations of resting steps. For Kunga, we zoomed on the South West section of the island (red square in the top right panel in (d)) where locations were recorded. (b,e) show the location-based UD up to 95% of the total utilization. It was estimated for each resting deer and is mapped with a color gradient from pure red, corresponding to highly used areas, to light yellow areas, corresponding to least used areas. (c,f) shows a 3-dimension representation of the same UD with height corresponding to intensity of use.

Deer ELI 06 in May 2011

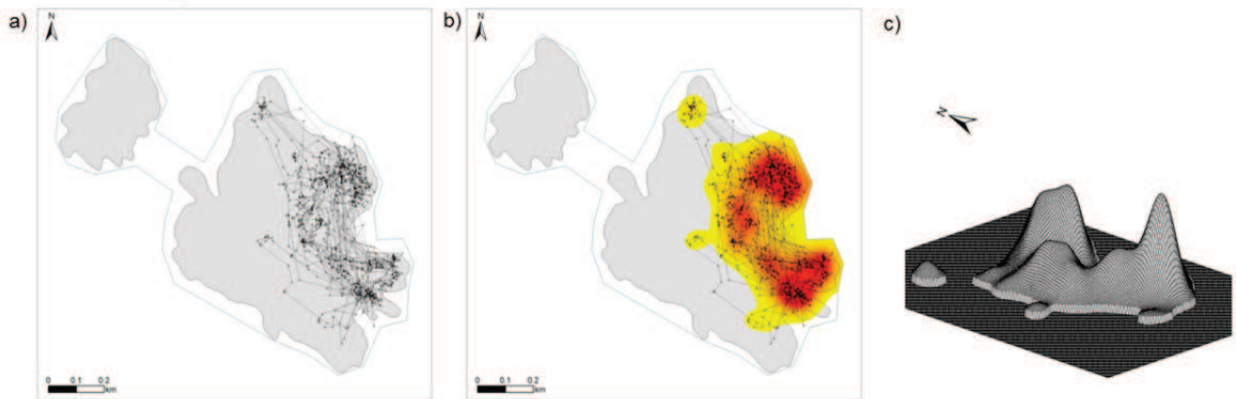


Figure CA.IV. 16: Examples of active utilization distribution (active UD) computed with movement-based kernel density estimation (KDE) for a deer on East Limestone (a,b,c) and on Kunga (d,e,f). (a, d) show active steps. For Kunga, we zoomed on the South West section of the island (red square in the top right panel in (d)) where locations were recorded. (b,e) show active UD up to 95% of the total utilization. It is estimated for each deer in activity and is mapped with a color gradient from pure red, corresponding to highly-used areas, to yellow, corresponding to least-used areas. (c,f) show a 3-dimension representation of the same UD, with height corresponding to intensity of use.

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DISCUSSION

In these four chapters we investigated how deer in heavily-browsed environment managed their food resource and predation risk (Figure 11). In particular, we highlighted that, on the study islands: i) deer could maintain abundant populations despite the apparent lack of resources in the understory, mainly by exploiting the subsidies from the canopy through litterfall and the annual growth of perennial rhizomatous plants; ii) deer did not develop chronic physiological stress despite their prolonged-exposure to low food abundance or predation risk, what we interpreted as behavioral and/or physiological adjustments mitigating deer exposure to stressors; iii) despite 60 years of isolation from any predators and over 100 years of isolation from wolves, deer maintained vigilance levels in lower ranges to those observed in deer populations exposed to predation risk, and they avoided feeding at bait stations scented with wolf urine. However, deer response to wolf cues was expressed mostly through changes in time exposed to risk rather than through increased vigilance; and iv) in a heavily browsed environment, predator-naïve deer presented two contrasted responses to a hunting for fear experiment: the deer that we were not able to capture (with baited traps) avoided the hunting area whereas the deer that could be captured continued to use bait stations and might have decreased their vigilance levels in the hunting area, although this last result should be confirmed.

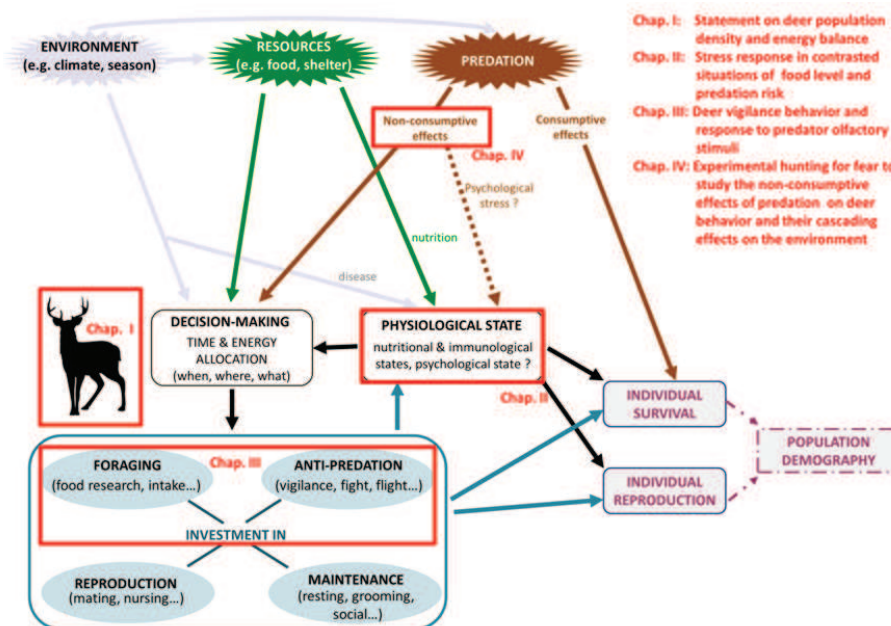


Figure 11: Overview of the contribution of this study to investigate how abundant deer populations manage their food resource and predation risk in heavily-browsed environment.

These results have been discussed individually in the relevant chapter. In this section, however, I revisit them all together by focusing on two axes: First, I stress the relative role of food and predation risk in the maintenance of abundant deer populations, based on the results we had obtained on risk management by deer in heavily browsed environment. Then, I explore how hunting, used as a management tool, could affect deer population in sites presenting similar characteristics than the study area, such as in many islands of the Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve and Haida Heritage Site.

I. EXPLAINING HIGH DEER DENSITY IN HEAVILY BROWSED HABITATS: WHAT DID WE LEARN?

I.A. THE ROLE OF FOOD

A remarkable result in this study was the finding that deer on East Limestone and Kunga (safe/poor islands) maintained a positive energy balance despite the missing understory (Chapter I). This was especially striking on Kunga where, despite some levels of uncertainties, our estimation of the amount of energy available was more than twice the estimation of the energy required for the maintenance of the population. Although such positive energy balances are possible because deer can shift their diet towards canopy litterfall and annual growth of perennial rhizomatous plants (Le Saout 2009), which both remain abundant, other factors may also contribute to explain these positive energy balances, possibly underlying even more the importance of food resources in driving deer population dynamics.

I.A.1. DEER BODY MASS AND REPRODUCTIVE TRAITS: ADJUSTMENT TO REDUCED FOOD RESOURCES?

Positive energy balance on East Limestone and Kunga may be explained by relatively low maintenance energy requirements when compared to other black-tailed deer populations in less depleted environment. Indeed, on East Limestone and Kunga average summer body mass was estimated to be c. 35 kg and c. 45 kg for adult females and males, respectively (Table I.1); whereas on Vancouver Island, B.C., Canada summer body mass was estimated to be c. 35-45 kg and c. 50-100 kg for adult females and males, respectively (Bunnell 1990), and on Channel Island, Alaska, U.S, those values were c. 32-45 kg and c. 35-52 kg, respectively (Parker et al. 1999). Reduction in growth may be interpreted as an adjustment to food limitation and has

been reported in white-tailed adult females living in heavily browsed forests which seem to maintain reproduction at the cost of growth (Simard et al. 2008, see introduction). Because on East Limestone and Kunga females seem to reproduce successfully (Chapter I), such an adjustment may have occurred in the study area what would support the importance of food resource in the current demography and life-history of the local deer populations.

In addition, although no detailed demographic data were available, our preliminary results suggested that most reproductive does were older than two years and that litter size was close to a single fawn per doe (Chapter I). On the continent, the first age at reproduction in coastal black-tailed does ranges between 1.25- and 2.25-year-old and does older than 2-years old produce on average 1.5 fawns, suggesting that twins are as common as singleton fawns (McTaggart Cowan 1956; Bunnell 1990). Similar results were reported for Sitka black-tailed deer, on Channel Island, Alaska, U.S., where of the five does older than a year, four reproduced and produced two singleton fawns and two sets of twins (Parker et al. 1999). This suggests that on East Limestone and Kunga deer reproduction may be limited by food (Bonenfant et al. 2009). In particular, this would follow Eberhardt's (2002) predictions according to which the age at first reproduction is delayed and female fecundity is decreased when food resources become scarce. This has been reported in other deer populations exposed to food shortages (review in Bonenfant et al. 2009).

I.A.2. MILD WINTERS: A FAVORABLE CONTEXT TO MAINTAIN HIGH-DENSITY POPULATIONS?

Mild winter conditions without heavy snowfall might favor the maintenance of high-density deer populations. Indeed, in a model of energy balance on Alaskan black-tailed deer, Hanley (1984) showed that snowfall could have a strong impact on deer energy balance mostly by limiting the amount of food available to deer and, to a lesser extent, by adding locomotion costs to animals, which are likely to limit their movements in presence of heavy snowfall (Parker et al. 1996). In our model of energy balance on East Limestone and Kunga, the energy available to deer in winter was already insufficient to meet deer energetic needs (Chapter I), and it seemed that in the study system summer was the critical time for deer to recover from the winter and store fat to prepare the next winter. The importance of summer was also reported in other deer

populations (e.g. Parker et al. 1999, 2009; Cook et al. 2004). It is thus unclear what the gain is for the local deer population to live in an environment with low snowfall. Mild winters might have only a moderate contribution to the maintenance of high deer density. This seems to be supported by the existence of other dense populations of *Odocoileus* deer in harsher climatic conditions (e.g. in Anticosti, Canada: Potvin et al. 2003; Tremblay et al. 2005).

I.A.3. SEAWEED: A RECIPE FOR HIGH-DENSITY?

The study area, however, is remarkable for giving access to marine subsidies to the local deer populations. Indeed on the study islands, deer feed on brown and red algae. Although seaweeds consist in only a small part of deer diet (c. 0-10%: Poilvé 2013), they may deserve to be considered for their nutritional values. Indeed, seaweeds, like *Alaria* species (present on the study sites), are as rich in energy as some fern species in summer (Applegate & Gray 1995; Parker et al. 1999). However, an efficient digestion of seaweeds is likely to require adapted microbial digestive flora, as observed in Orkney sheep (*Ovis aries*) feeding almost exclusively on seaweeds (Orpin et al. 1985). In addition seaweeds are also rich in salt. While salt may be a reason making seaweeds attractive, consuming them is also likely to require some physiological adjustments to excrete excess salt and to allow maximizing the value of seaweed as a food resource (Applegate & Gray 1995). It would thus be interesting to better assess the contribution of seaweed as energy resource for study deer, especially at winter time, when the energy available by terrestrial plant is limited (Chapter I).

Seaweeds are also recognized for their richness in vitamins and minerals, like calcium, potassium, vitamin D or iodine, which may promote animal reproduction (Chapman 1950; Burtin 2003). For example, lactating cows fed with a diet enriched with seaweed (*Ascophyllum* species) were shown to increase their milk production (Nebb, 1967 and Jenson et al. 1968 in Chapman 1950). However this is not always the case (Lunde & Closs 1936 in Chapman 1950) and/or the effects of seaweeds might be difficult to detect. For example, sow and piglets fed with kelp tended to have larger litter size and body mass at birth, respectively, but this was not significant (Kim et al. 2011). Whether dietary seaweed may affect the reproduction of deer by providing complementary nutriments may be an appealing idea. Nonetheless, to my knowledge,

this has never been mentioned in ungulates feeding on seaweed (Orkney sheep: e.g. Orpin et al. 1985; Balasse et al. 2005; Hansen et al. 2003; red deer: Conradt 2000). A positive effect of seaweed on individual reproduction may thus not be relevant for ungulates, although it might not have been tested in ungulates properly.

The positive effect of seaweed consumption on the immune system may be less controversial. In a non-systematic review of the impact of seaweed consumption on animal immune systems, I found eight studies, including a review, and all focusing on livestock (Table 1). Among them, seven found a positive effect of dietary seaweed on immune functions whereas a single one (on lambs) found an inhibitory effect of dietary seaweed on the immune systems. It would thus be interesting to test if seaweeds could enhance the immune system in the deer studied and then, if this could contribute to the maintenance of abundant populations.

Table 1: Non-systematic review of the effect of dietary seaweed on the immune system of animals. The herbivore species, the seaweed species (ANOD: *Ascophyllum nodosum*) or group of species (kelp) used to fed the individuals, the effect of the dietary seaweed on the immune system (positive when it enhances it; negative when it inhibits it), the description of the effect of the diet on the individuals as described in the article (Ig: Immunoglobulin), and the reference (Ref.) are provided for each study.

Animals	Seaweed	Effect of dietary seaweed on the immune system	Description of the effect of dietary seaweed on the immune system	Ref.
beef steer	ANOD	+	• increase cell-mediated immune function	1
beef steer	ANOD	+	• increase cell-mediated immune function	2
goat	ANOD	+	• improve the anti-oxydant statut	3
goat	ANOD	+	• improve the anti-oxydant statut	4
lamb	ANOD	+	• increase cell-mediated immune function	5
lamb	ANOD	-	• suppression of IgG and IgM production	6
sow & piglet	kelp	+	• increase the production of lymphocyte , IgG, IgA and IgM • reduce the concentration of the minimum inhibitory dilution measure of rare cells and a number of precursors or white cells (MID concentration)	7
beef steer & pig	ANOD	+	• increase cell-mediated immune function	8

References: 1: (Allen et al. 2001a); 2: (Saker et al. 2001); 3: (Galippli et al. 2004); 4: (Kannan et al. 2007); 5: (Saker et al. 2004); 6: (Archer et al. 2007); 7: (Kim et al. 2011); 8 : (review in Allen et al. 2001b).

Despite these potential positive effects, it has been suggested that intense and/or long-term consumption of seaweed might be deleterious to animals, particularly due to the presence of arsenic components in some seaweed species or due to an excess of iodine consumption (Paulikova et al. 2002; Hansen et al. 2003). In the present study, because seaweed consumption is limited, such negative effects are unlikely to occur. For the same reason, positive impacts on deer reproduction and immunity may also be anecdotal. However, this highlights some possible research perspectives to better assess the potential effect of dietary seaweed on deer physiological status and how this may affect deer population.

I.B. THE ROLE OF PREDATION RISK

I.B.1. SAVING VIGILANCE COSTS?

Another remarkable result of the present study was the maintenance of overt vigilance in predator-free deer, even when food had not to be searched for (when bait amount was high) and when food could be ingested without lifting the head (calibrated bait) (Chapter III, Part I). Consequently, it seems that the absence of predation did not release deer from vigilance costs, although a firm conclusion on this would require more accurate assessment of how chewing is organized in relation to vigilance bouts. The importance of predation costs have been discussed in Chapter III, Part I. Of course one may argue that in presence of predation risk deer would increase vigilance (Lima & Dill 1990) and hence that the cost expected to be saved by predator-free deer should be the difference between the one expressed in presence of risk and the one expressed in absence of risk. This would be the ideal situation. However, vigilance may not be as expensive as expected (Fortin et al. 2004) and deer seemed to manage risk more by adjusting the time spent in risky place than by vigilance (Chapter III, Part II). It seems thus, that the gain in vigilance due to the absence of predation may be only limited in the study area.

I.B.2. FREE FROM SPATIAL CONSTRAINTS?

It is interesting to note that in the study area deer seemed fairly consistent in the use of spatial avoidance as anti-predator strategy: deer on Reef did not seem to develop a chronic

physiological stress in presence of human activities assimilated to predation risk, but seemed to avoid human areas (Chapter II). On East Limestone deer limited the time spent at bait stations in presence of wolf urine (Chapter III, Part II). On Kunga unmarked deer avoided the hunting area (Chapter IV), and marked deer might have decreased their levels of vigilance at the bait station in the hunting area what might be interpreted as a spatial management or risk allowing deer to limit the time they spent in the hunting area (Brown 1999) (Chapter IV, CA.IV.B). However, this last observation should be confirmed. The absence of predators may thus have released the spatial trade-off faced by deer between risky and safe places, and might have limited costs associated to the missing opportunities to feed or to travel (e.g. between resting and foraging sites). However, at this stage costs cannot be estimated and this hypothesis cannot be tested. This, nevertheless, offers interesting perspectives for future study based on GPS data.

For example, mule- and black-tailed deer mothers are known to display various anti-predation behaviors, such as putting distance between their fawn(s) and their foraging sites (Geist 1981; review in discussion Ozoga & Verme 1986). Comparing the spatial use of deer mothers on East Limestone and Kunga with the one of black-tailed deer mothers on other islands in presence of predators (e.g. in Vancouver Island: McNay 1995) may contribute to better inform this aspect. In addition, if predator-free deer mothers are freed from the need to select distant sites for fawn bedding and adult foraging, one may expect such does to save travel time and hence to be more efficient in rearing their fawn(s). Comparing fawn body mass gain, fawn weaning age, length of time the fawn is left hidden and the type of fawn bedding sites selected by deer exposed to contrasted levels of predation risks and food (e.g. Clutton-Brock et al. 1983, 1987; Ozoga & Verme 1986; Verme 1989; Andersen et al. 2000; Therrien et al. 2008) may prove essential to better assess the relative importance of resource level and predation risk in explaining deer maternal behavior. Interestingly, a current research project is studying fawn survival and conditions in presence of its natural predators (i.e. wolves, brown and black bears) on Prince of Wales Islands, Alaska (c. 200 km North from the study area) (Person 2010). This might offer some research opportunities to compare deer maternal behavior between deer living in the predator-free study area and those living on other islands in presence of natural predators.

I.B.3. FREE FROM GROUP COMPETITION?

Mule deer are known to bundle when in the vicinity of a natural predator such as a coyote for instance (Lingle & Wilson 2001; Lingle & Pellis 2002; Lingle et al. 2005). However, grouping is also expected to increase conspecific competition. In the absence of predation risk, deer would be expected to spare this cost and this may favor deer dispersion over the island, limiting thus individual competition and delaying density-dependence mechanisms. This could not be assessed here, however, GPS data on Kunga and Reef (islands with comparable areas) could provide interesting insight in terms of animal territoriality at small (e.g. days) and larger (e.g. season) temporal scale.

To conclude this section there are many evidences (of various strength) to underline the key importance of food resources to explain the current dynamics of the deer populations. This has to be linked to the remarkable ability of deer to cope with different levels and different kinds of resources. Regarding the role of the absence of predation risk, the pattern is unclear and many questions remain. We focused on vigilance, as anti-predation behavior, and in this study we could not detect a significant cost associated with it, suggesting that in terms of costs saved via vigilance the absence of predation may have only a very limited impact. Spatial use may show a different pattern and offers new perspectives. It is interesting to note that predation risk have been reported to affect the population dynamics of birds and insects (e.g. Peckarsky et al. 1993; Schmitz et al. 1997; Zanette et al. 2011, 2013 but see introduction) but seemed more difficult to identify in large herbivore population, like deer (Middleton et al. 2013). The absence of predation may have been a “facilitator” allowing deer to have access to any resources available on the island with no spatial restriction. How much food and risk, respectively affected this pattern, however, remain largely unknown and offer interesting research perspectives.

After having reconsidered how our study contributed to better understand what may explain the maintenance of high deer densities in a heavily browsed environment, I now look forward and focus on deer management and in particular on hunting as a management tool. For this exercise, I will consider deer management in predator-free places, like islands in Laskeek Bay or

potentially some islands of the Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve and Haida Heritage Site. I will then conclude by broadening my considerations. This choice was motivated by my wish to warrant the practical relevance of my results. The following section is *not a prediction* of what would happen should hunting take place on some of these islands. It is an *exploration* of how some processes may influence the dynamics of the ecosystem in this context, and it should be considered as such only. In the following discussion I assume that unmarked deer are deer avoiding the hunting area and could be assimilated to shyer deer, less tolerant to humans than marked deer which are those remaining in the hunting area and which could be assimilated to bolder deer (Box 6, Chapter IV). This, however, remains a working hypothesis resulting from our interpretation of deer capturability (Box 6) and response to our hunting for fear experiment (Chapter IV).

II. A THOUGHT EXPERIMENT: HUNTING AS A MANAGEMENT TOOL FOR ABUNDANT DEER POPULATIONS IN PREDATOR-FREE PLACES

In such heavily browsed environments, where deer have dramatically reduced the local forest biodiversity, a relevant management goal may be to limit and reduce deer impact (Gaston et al. 2008). Considering hunting as a management tool¹, the objective will be triple: i) maximize the consumptive effect of hunting; ii) maximize the non-consumptive effects of hunting; and iii) minimize the economic costs associated with the hunting effort needed to achieve the two former objectives. The question is now: how can we achieve this? To contribute an answer to this question I consider what would happen if hunting occurred in the study area. Within this framework, our hunting for fear design (Chapter IV) should be considered as a theoretical approach only because hunters would not fake shooting to scare deer, but simply aim at killing (Chapter IV) when management objectives include both maximizing non-consumptive and consumptive effects of hunting. In the following scenario, one should imagine that deer individuals that we scared would actually face real hunters. Could those deer have survived to an encounter?

¹ Note that here I skipped the step of inventorying all management tools available and considered only hunting.

II.A. THE FATE OF BOLDER INDIVIDUALS

There might be a chance for those deer to survive, but this seems very unlikely. Most deer flight distances were around 10-15 m, which strongly suggest that most deer would have been killed by hunters. Indeed, 5-10 m was estimated to be the threshold distance at which a deer prey is likely to be caught by a natural predator (Stankowich 2008), and natural predator cannot even kill their prey from a distance. According to the hunter ability these deer might survive but skilled hunters are expected to not miss a prey at c. 10-15 m (e.g. Kilpatrick et al. 2002). Consequently, most deer remaining in the hunting area (bolder deer) are likely to be eliminated from the deer population fairly quickly.

II.A.1. COULD THEY ESCAPE BY LEARNING?

This result should nevertheless be nuanced, because it assumes that bolder deer could not learn nor adjust their behavior and after some time avoid the hunting area. However, if in presence of a doe and its offspring, hunters targeted the offspring first, as suggested by Cromsigt et al. (2013), then adults might be able to learn. This has been shown in predator-naïve moose in Yellowstone National Park (Berger et al. 2001). In this study, mothers, whose calves were predated by wolves, changed their behavior and avoided predator cues unlike other mothers whose calves were not predated. Deer thus seem able to learn (see also Ozoga & Verme 1986) and bolder individuals might have the opportunity to adjust their behavior. However, such a hunting tactic (e.g. sparing does) may not be relevant with regards to the main objective of the hunt which is to limit deer impact. In addition, learning may also interact with animal genetics and previous experiences (e.g. Curio 1993; Griffin et al. 2001; Griffin & Evans 2003; Griffin 2004; Lima & Steury 2005; Ferrari et al. 2012) and the temporal window and circumstances needed for deer to learn and possibly adjust their behavior remain to be better defined and investigated.

Whether bolder individuals can learn or not, should however not affect the prediction that hunting should select against bolder individuals. If bold/shy is a personality, defined as consistent inter-individual behavioral differences over time and/or context (Réale et al. 2007) then bold deer would be expected to remain bold with little hope for learning and would be eliminated. If bold/shy is a flexible behavioral trait that may be adjusted over time and contexts

then bold behaviors would also disappear in favor of learnt shyer behavioral strategies, at least regarding deer response to hunting. In both situations bold behaviors are thus expected to be eliminated from the populations in presence of hunting. Considering that, in our study sites, some individuals could be recaptured (Box 6) and scared several times (Chapter IV) this tends to support the hypothesis that bold/shy behaviors could be personalities. In the following reasoning, my working hypothesis will thus be that bold/shy individuals represent different personalities although this remains a hypothetical framework.

II.A.2. COULD PERSONALITIES PERSIST VIA BEHAVIORAL SYNDROMES?

Behavioral syndromes means that some behavioral personality-defining traits are correlated (Sih et al. 2004). For example, Réale et al. (2000) showed that among a population of bighorn ewes in Alberta, Canada, bolder bighorn ewes tended to be less docile. Interestingly, younger and bolder individuals were more likely to survive cougar predation than older or shy individuals, but younger and less-docile individuals were also more likely to survive cougar predation than older and non-docile individuals (Réale & Festa-Bianchet 2003). Because bold-non-docile and shy-docile ewes were equally selected by cougar predation, both bold/shy and docile/non-docile personalities were maintained in the population even if shyness and non-docility were selected-against by cougar predation.

According to this example, both bold/shy personalities may persist in a population if hunting selects against shy individuals via a behavioral syndrome. I explored this possibility and considered a set of correlations between neuroendocrine and behavioral traits, defining coping-styles (Koolhaas et al. 1999). Two main coping-styles have been described: proactive and reactive coping styles (Box 7). On the one hand, proactive individuals are expected to be bolder, more active and more eager to fight or flight in response to a threat. On the other hand, reactive individuals are expected to be shy, less active, and more eager to freeze or hide in response to a threat (Box 7). The current data available did not allow to test this hypothesis properly; however, an exploratory analyses suggested that some behavioral traits might be correlated (Box 7). In the following reasoning I explore how some correlations, if they exist, could affect the maintenance/elimination of bolder individuals in the deer population.

Two syndromes may be particularly relevant for the present study: First, bolder individuals may either fly or fight in response to a threat, whereas shyer individuals might either freeze or hide. Within this framework, bolder individuals which flight early or shyer individuals which remain hidden should avoid being killed by hunters more often and thus these “syndromes” will be selected into the population. Bolder individual which fight will be killed and should be counter-selected. If such correlations exist then two kinds of deer may be selected through hunting: the shy deer hidden in refuges and the bold but fly-early deer which may remain in the hunting area if they succeed in detecting hunters early enough to escape. Most flight distances conducted on marked deer were less than 15 m but some marked deer flew at distances greater than 20 m (CA.IV.C). Whether such a difference in flight behavior may make a difference in the survival of bold deer is unknown, but it suggests that some bold deer might remain in the area despite the hunt. However if bolder deer are also more active, then they might be able to flight early but might also be detected more easily (e.g. Ciuti et al. 2012), and this would contribute to limit the frequency of bolder individuals in the population. This exercise could be repeated with other correlations.

Overall this coarse exploration intended to show that, despite the selection pressure induced by hunting, there are mechanisms which may explain the maintenance of some levels of variability among behavioral traits (Sih et al. 2004; Wolf & Weissing 2012; Foster 2013; Sih 2013), and phenotypic traits in general (Whitham et al. 2006; Siepielski et al. 2009; Dingemanse & Wolf 2013). However, in the present study case, because bolder individuals which remain in the hunting area have more chance to encounter a hunter and to be killed than shyer individuals hidden in refuge areas, I will assume that bolder behaviors will overall become rarer than shyer behaviors among the individuals which survive.

BOX 7: A preliminary assessment of deer coping styles in the studied populations

Many studies have considered the correlation between physiological and behavioral traits (e.g. Wingfield 2003, 2013; Biro & Stamps 2010; Coppens et al. 2010; Clinchy et al. 2013; Angelier & Wingfield 2013 but see introduction II.C.3). In particular, Koolhaas et al. (1999) highlighted some consistent correlations between neuroendocrine and behavioral

traits which he named “coping-styles”. Two main coping-styles have been described: the proactive and reactive “coping styles”. For the sake of greater clarity, note that “coping style” considers only correlations between neuroendocrine and behavioral traits. This concept may be extended to correlation between metabolic, hormonal and immunity traits.

BOX 7 (continued)

It is called “pace-of-life syndrome” and was initially developed to characterize population or species and not individuals *per se* (Réale et al. 2010).

Coping styles have been described in birds (Cockrem 2013) and mammals (Koolhaas et al. 1999) and may be explained, at least partially, by neuronal and/or physiological mechanisms (Biro & Stamps 2010;

Coppens et al. 2010). Recently, Cockrem (2013) revisited and synthesized this proactive/reactive coping style concept (Table B7.1). I used this theoretical framework, to explore if the physiological and behavioral measurements obtained on deer from East Limestone and Kunga could suggest that such correlations exist among deer traits.

Table B7.1: Behavioral characteristics in relation to proactive and reactive coping-styles (adapted from Cockrem 2013).

	PROACTIVE	REACTIVE
Behavioral Response	Fight/Flight	Freeze/Hide
Behavioral Style	Aggressive – bold	Non-aggressive – shy
Exploration	Fast – superficial	Slow – Thorough
Behavioral flexibility	Rigid – routine-like	Flexible
Fearfulness (nervousness)	Less nervous	More nervous
Glucocorticoid levels * (baseline and responsiveness to an acute stressor)	Relatively low	Relatively high
Success in variable and unpredictable environments compared to more constant environments	Lower	Higher
Body temperature in response to handling stress**	Lower	Higher

* detailed in Koolhaas et al. (1999) and reviewed by Wingfield (2003) and by Coppens et al. (2010)

**added according to Carere & Van Oers’s results on great tits *Parus major* (2004)

A comparison between unmarked and marked deer would likely have provided a good gradient of proactive/reactive coping styles. However, the current dataset on unmarked deer was insufficient to properly conduct this comparison. Rather, based on fieldwork observations I identified *a priori* three marked females on each island which may present different coping styles. For example, on Kunga, deer K 05 was observed daily at the campsite, could be followed closely to calibrate activity sensors (Chapter IV), and was scared 19 times during the hunting for fear experiment without marked responses (Chapter IV). Deer K 07 spent c. 40-50% of her active time in windfall areas (Chapter IV) and was observed less often close to human activities. Deer K 09 was generally detected in the interior forest and rarely close to the campsite. Deer K 05 might thus be slightly more proactive than deer K 07 or deer K 09. Based on similar approach, I identified three females on East Limestone.

For each deer I considered six variables: i) the number of capture sessions when the individual was captured (inter-session capturability: min=1, max=3);

ii) the number of recaptures during the capture session in August-October 2011 (intra-session capturability: min=0, max=23); iii) the proportion of visits with at least an aggressive event (i.e. chasing another deer, Figure B7.1) between March and June 2012 at bait stations (aggressiveness: min =0%, max =17%); iv) the average proportion of time spent in overt vigilance (*sensu* Chapter III) at bait stations at daytime in March-June 2012 (vigilance: min = 0%, max =83%); v) the first flight distance measured on a given individual when it was not resting (flight distance: min = 2 m; max =37m); vi) the fecal glucocorticoid metabolite levels (FGM levels) assessed in samples collected on animals during the captures in August-October 2011 (FGM levels: min =10 ng/g, max=51 ng/g); vii) anal temperature measured at the end of deer handling during the capture session in August-October 2012 (min = 36.9 °C; 40.7 °C). Indeed, body temperature may reflect an animal’s reaction to a stressful event (e.g. handling) (Carere & van Oers 2004). Therefore, I used anal body temperature as a possible index of individual stress response to an acute stressor.

BOX 7 (continued)



Figure B7.1: Example of deer aggression observed at bait stations: (a), (b) Aggression between two collared does on Kunga in May 2011 at daytime. (c),(d) Aggression between a marked subadult female and a collared doe on Kunga in May 2012 at night

For each variable I identified the minimum and maximum values assessed for deer populations in pooling the dataset from both islands. To compare this suite of traits among individuals I rescaled each measurement so that the extreme values would be equal to 0 and 1. I arbitrarily decided that 0 would correspond to values expected for proactive coping-style and 1 for reactive coping-style. For example, proactive animals are expected to be more aggressive. In this case the maximum level of

aggressiveness recorded was rescaled to be equal to 0 and the minimum level would be equal to 1. On the contrary, proactive animals are expected to be less responsive to acute stressors, they should thus show lower anal temperature. In this case the minimum value recorded for anal temperature was equal to 0 and the maximum to 1 (Table B7.2). This allowed assessing possible trends in animal behavior according to the proactive/reactive coping style (Figure B7.2)

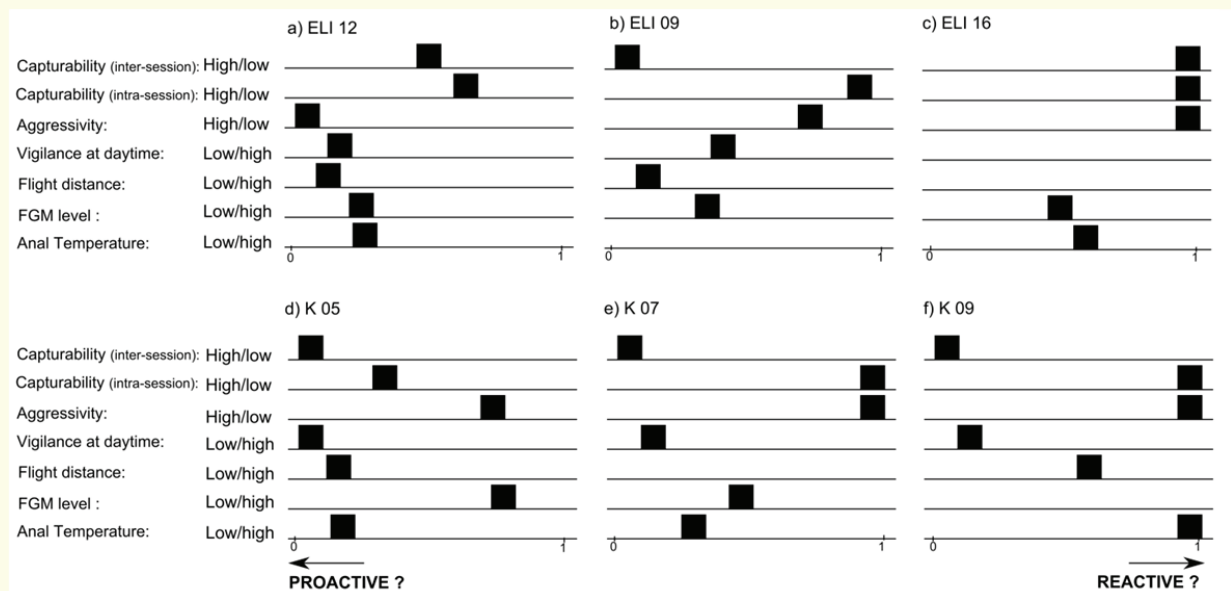


Figure B7.2: Example of physiological and behavioral traits measured on six deer, three on East Limestone (a,b,c) and three on Kunga (d,e,f). Six traits are considered: inter-session capturability, intra-session capturability, aggressiveness, vigilance level, flight distance, fecal glucocorticoid metabolite level (FGM level) and the anal temperature. Numerical values of traits are ordered so that values expected for proactive coping -style would be close to 0 and values expected for reactive coping-style would be close to 1. When data were not available the row remained empty. See Table B6.1 for the prediction on each coping style and see text for a detailed presentation of each variable.

BOX 7 (continued)

Given the dataset considered, this brief analysis should just be considered as an exploratory analysis. Although no strong pattern emerged, I noted that on East Limestone the pattern observed may agree with the *a priori* classification (deer ELI 12 being more

proactive than ELI 16) and that on Kunga K 05 might be slightly more proactive than K 09, as expected. A proper validation is obviously required on a larger data set and might consider other personality traits (e.g. sociality, neophobia).

In this last section, I explore what the consequences of such a selection (against bolder individuals) would be on deer-environment interactions and how this may match with the initial management goal.

II.B. CONSEQUENCES OF THE REMOVAL OF BOLDER DEER ON DEER IMPACT ON THEIR ENVIRONMENT

II.B.1. DEER WITH ACCESS TO REFUGES

II.B.1.a. Temporal extent of hunting

If the boldest deer are eliminated by hunting, then the remaining deer (mostly shy individuals) are expected to remain in refuge areas. Indeed, in Chapter IV we showed that unmarked deer (shyer deer) tended to avoid the hunting area at day and night-time during both the hunted and the non-hunted days. This suggests that these deer would remain in refuge areas if facing hunting efforts similar to the one of our experiment (2-3 hunted days spaced by 3-4 non-hunted days). Generalizing this result remains delicate because deer response is likely to vary with the hunting effort (i.e. duration, frequency of hunting events) (Kilpatrick et al. 1997) and hence would require some calibration between areas to assess the optimal hunting schedule to obtain a complete exclusion of deer from a given area. In particular, deer have been reported to return into the hunting area within a few days following the end of the hunting season (Vercauteren & Hygnstrom 1998; Kamei et al. 2010). In our hunting experiment deer may have tended to come back during the posthunt period (i.e. within 13 days of the end of the experiment; Chapter IV). Overall, this seems to suggest that to protect a given area from deer browsing pressure, a regular and constant hunting effort (e.g. a day of hunting spaced by a few of non-hunting Kilpatrick et al. 1997) may be required.

The hunting effort may be modulated as a function of the management goals for vegetation recovery. Indeed, plant response to browsing pressure is species-dependent (Augustine & McNaughton 1998). Less intense hunting efforts will be required to allow the recovery of plant species less-preferred by deer or more tolerant to medium to low browsing pressure while the recovery of deer-favorite plant species or plant species less tolerant to browsing pressure (e.g. in the study area Gaston et al. 2008; Chollet 2012) which are usually the focus of management plans (e.g. redcedar management in the study area Wiggins 1996) may require prolonged exclusion of deer from a given area or to protect individual plants from deer browsing.

Measuring giving-up density (Brown et al. 1999; Brown & Kotler 2004) in both refuges and the hunting area may be a tool allowing to assess the overall level of risk perceived by deer and to calibrate the hunting effort required to limit deer presence in a given area. This may be particularly appropriate as, under the current scenario, after having eliminated bolder individuals hunters will meet deer rarely and the hunting effort (number of animal killed) in the hunting area may not reflect the level of risk perceived by deer and hence may not inform on how deer may use the hunting area.

II.B.1.b. Spatial extent of hunting

The choice of the extent of the hunting area is probably as important as the hunting effort required. Implicitly, I assumed that if hunting is restricted in area this will result in non-hunting refuge areas used by deer while the hunting would become less exposed to deer browsing. In this scenario, a hunter could be seen as an ambush predator that would remain in a given area identifiable and avoidable by deer (Preisser et al. 2007; Schmitz 2008). In the medium- to long-term such a design would have severe consequences on the refuge area structure and composition as deer browsing pressure would be concentrated in this area (Orrock et al. 2012). The underlying question becomes: is it acceptable to protect a given area to the detriment of another?

Density-dependent mechanisms are theoretically expected to be high in the refuge area (Pallini et al. 1998; Preisser et al. 2007, 2009; Orrock et al. 2012), as more individuals concentrate on

fewer resources which will be depleted on the long-term. This ideal scenario would maximize the non-consumptive effect of hunting. However, in Chapter I we stressed the high potential of temperate forests to meet the needs of abundant deer populations through food supplies which production was not directly affected by browsing (e.g. litterfall). This seriously questions the long-term future of deer refuge areas and the possibility to manage deer via non-consumptive effects in refuge area. Indeed, in introduction I described the dramatic ecological impacts deer can have when overabundant and the remarkable ability of deer to cope with the situation. Although the scale considered here is reduced to refuge and hunting areas, similar outcomes, such as the reduction in the local biodiversity and the maintenance of high densities of deer locally feeding on litterfall or perennial rhizomatous plants, might occur questioning thus the relevance of this strategy with regards to the management goals.

II.B.2. DEER WITHOUT REFUGES

To avoid the problem of possibly “sacrificing” deer refuge area, one may consider extend the hunting area so to prevent the occurrence of refuge areas (e.g. Kilpatrick et al. 2002). This should spread out the impact of deer browsing over the whole area of interest and limit a more severe depletion of a given refuge area (Gude et al. 2006). In this case, hunters would be assimilated to stalking predators and theory predicts that the main impact on the prey population would be via the consumptive effect of predation (Preisser et al. 2007; Schmitz 2008). Hunting effort, here, may thus be a relevant index of the efficiency of hunting to limit the deer population. However, this raises the classic challenge of hunting as a management tool (e.g. accessibility, efficiency, acceptability (Nugent & Choquenot 2004; Raik et al. 2005; Nugent et al. 2011, see introduction Chapitre IV).

II.B.3. LESSONS LEARNT FROM THIS THOUGHT EXPERIMENT

Both management scenarios (i.e. restricted or unrestricted hunting area) have advantages and disadvantages and may be understood as a simplified view of the use of non-consumptive or consumptive effects of predation as main management tools. The scenarios described above are extreme cases and in a real situation some refuges are likely to always exist (Grau & Grau 1980; e.g. Kilpatrick et al. 2002; Scillitani et al. 2009; Bonnot et al. 2013) and the main question may actually be what is the relative proportion of the area to manage that could be accessible and hunted in relation to the resource each area may offer? If this is a small proportion then hunting may be more likely to result in the former “refuge scenario” depending more on the non-consumptive effects of hunting to mitigate deer impact on their environment. In this case, defining clearly the future perspective for refuge areas may be highly recommended to avoid future conflicts. For example in the Greater Yellowstone Area, U.S., elk avoided hunting areas by seeking refuge on private rangelands resulting in problems for landowner whose livestock pasture were used by elk (Proffitt et al. 2009). Conversely, if a large proportion of a given area is hunted then the consumptive effects of hunting may become the major mechanism affecting deer populations, but this may not always be feasible and/or efficient (Simard et al. 2013).

Broadening these coarse exploratory scenarios should be done cautiously. Indeed, the discussion on deer personalities and medium- to long-term response of deer to hunting has been based on results obtained on predator-free islands, where very bold individuals were present. However, in other contexts where hunting, meso- and/or top-predators are present, those bold individuals are likely to have been already eliminated by predators and hence the range of behavioral traits among individuals and of the alternative behaviors may be different among the study area and other sites. In particular, deer perception of risk and decision-making on food and risk may be different and hence is likely to result in different management outcomes and challenges. For instance, in the scenarios I considered, deer remained for long periods of time in refuges. But in many places refuge areas do not provide enough resources for deer, and deer will manage their use of space at a fine temporal scale, maximizing their income and minimizing their risk while using both refuge and non-refuge areas (e.g. Kilgo et al. 1998; Bonnot et al. 2013). In addition, the present reasoning is very limited and only tentatively draws

a possible set of outcomes with regard to hunting as a management tool for deer. Many other approaches exist and have been used to tackle this question (e.g. Hansen & Beringer 1997; Woolf & Roseberry 1998; Nugent et al. 2011; Urbanek et al. 2011). I hope this simple exercise will however have provided some insights, and some questions that should be considered before using hunting as a management tool.

Recent works have suggested ways to provide a general theoretical framework for assessing the relative impact of consumptive and non-consumptive effect of hunting on prey. For example, Creel (2011) suggested that one could predict the severity of predation risk on prey based on the characteristics of the prey to manage (e.g. prey diet (generalist vs. specialist) or prey reproduction strategy (r- or K-strategy)). This overall framework complements Schmitz's (2008) and Preisser's (2007) works. They suggested that the behavior of the predator may be used to predict the impact of predation risk on the prey population. This ongoing research highlights the current search for general rules which may ease decision making in management. Many challenges remain but, as mentioned by Woolf & Roseberry 1998, "we have been effective deer managers and our management paradigms have served the resource well". There are thus good reasons to think that "we" can overcome these challenge and continue to be "effective deer managers".

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APPENDIX A: A BETTER WORLD FOR BRYOPHYTES: AN OVERLOOKED POSITIVE COMMUNITY-WIDE EFFECT OF BROWSING BY OVERABUNDANT DEER

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Submitted to Ecoscience

KEYWORDS: Cervidae, forest ecosystems, herbivore selectivity, overabundance, plant tolerance

ABSTRACT

During the twentieth century populations of several deer species (*Cervidae*) increased dramatically in temperate and boreal forests worldwide leading to major changes in forest plant and animal communities. The consequence of deer overabundance on their understory vegetation has been documented repeatedly. In situations of severe browsing pressure, even the least palatable vascular plants were negatively affected. However, deer impact on bryophytes has been greatly under-investigated despite their key role in ecosystem functioning and their high conservation profile. Taking advantage of a unique situation involving adjacent islands with and without deer that resulted from the introduction of black-tailed deer (*Odocoileus hemionus*) on the Haida Gwaii archipelago (British Columbia, Canada) we explored the response of the bryophyte community to unregulated browsing. We compared species density, cover and diversity between islands never colonized by deer and islands with prolonged deer presence. We took a novel approach that combined direct observations of deer foraging with sampling of the vegetation. We show that even in situations of severe browsing pressure deer totally avoided bryophytes. Contrary to what is observed for vascular plants (even for tolerant species such as graminoids), species cover, species density and diversity of bryophytes were higher in the presence of deer. We attribute this dramatic increase to reduced competition with vascular plants especially for light.

INTRODUCTION

The impact of herbivores on plant community composition results from the interaction between plant resistance strategies (e.g. tolerance and avoidance) and herbivore selectivity (Milchunas, Sala & Lauenroth 1988; Augustine & McNaughton 1998; Milchunas & Noy-Meir 2002). Plant tolerance, defined as the ability of plants to respond to herbivory in terms of growth, reproduction or survivorship, has been explained as the result of the co-evolution between plant physiology and/or morphology and grazing and/or browsing by animals (McNaughton 1984; Olf & Ritchie 1998).

Plant avoidance, defined as the ability of a plant to avoid being consumed, provides plants with varying levels of protections from herbivores (Milchunas & Noy-Meir 2002). The proportion of plant species able to tolerate and/or avoid herbivory is predicted to increase in a community with increasing intensity of herbivore pressure (Cingolani, Posse & Collantes 2005).

Plant tolerance and avoidance will lead to selective foraging by herbivores which can, in turn, change plant community composition. Selective browsing or grazing by ungulates on preferred species can for instance confer a competitive advantage to unconsumed species, allowing them to increase in abundance to the point of becoming dominant (Augustine & McNaughton 1998).

In addition to consumptive effects, herbivores can also modify plant communities by changing nutrient availability. The provision of feces and urine accelerates nutrient cycling, particularly for nitrogen, which can favor species able to use it quickly (competitive species, Harrison & Bardgett 2008).

Finally, the mechanical effects of trampling by large herbivores can directly damage plants (Kirby 2001; Pellerin, Huot & Côté 2006) reducing their occurrence and cover while increasing cover of bare soil and thus facilitating seedling establishment in some species (Stammel & Kiehl 2004). Impact of herbivores' presence will thus depend on the characteristics of the plant species present (Olf & Ritchie 1998).

In temperate and boreal forests worldwide, efforts to understand the response of plant communities to herbivory have been steadily growing since the second part of the 20th century in response to the increase in deer (*Cervidae* family) populations (North America: Côté et al. 2004, Europe: Fuller & Gill 2001, Latin America: Flueck 2010, Japan: Takatsuki 2009, New

Zealand: Wardle et al. 2001). These increases in cervid populations caused dramatic modification in forest understories, affecting plant community abundance and composition (e.g. Augustine & deCalesta 2003; Rooney & Waller 2003) as well as the animal guilds that depend on them (e.g. Miyashita, Takada & Shimazaki 2004; Chollet & Martin 2013). Long term studies, such as those of Horsley, Stout and deCalesta (2003) in Pennsylvania, documented a decrease in the abundance of most plant species except those that could tolerate severe defoliation, such as graminoids (e.g. Kirby & Thomas 2000; de la Cretaz & Kelty 2002; Rooney 2009), or those that were avoided by deer such as ferns, sedges, and black cherry *Prunus serotina*, which increased. Based on these results Rooney (2009) suggested that the increase in cervids could lead to a large scale forest understory biotic homogenization characterized by a dominance of graminoid species. Bryophytes are generally considered as avoided by herbivores because of their low digestibility associated with their high concentration of lignin-like compounds (Prins 1982). Furthermore, bryophytes, in contrast to vascular plants, are considered to be more limited by light than by nutrients (Kull, Aan & Soelsepp 1995; Bergamini & Peintinger 2002). Any decrease in vascular plant cover (or abundance) should thus promote bryophyte establishment and growth as a result of decreased competition for light. While studies on the impacts of grazing and trampling on bryophyte cover and species richness have been carried out in Arctic ecosystems (e.g. Pajunen, Virtanen & Roininen 2008) and in temperate grasslands (e.g. Takala, Tahvanainen & Kouki 2012), surprisingly few studies have looked at their response to high levels of herbivory in boreal or temperate forests despite of their high abundance and the richness of this plant community (Glime 2007).

We took advantage of the unique natural experiment that resulted from the introduction of black-tailed deer (*Odocoileus hemionus sitchensis*) to the Haida Gwaii archipelago to investigate the effects of herbivore presence on the composition and structure of the bryophyte community. On these islands, introduced deer dramatically reduced tree regeneration and the extent of understory vascular plant cover (Martin & Baltzinger 2002; Stockton et al. 2005; Martin et al. 2010). We used a subset of islands with and without deer to directly assess 1) how attractive bryophytes were to deer; 2) how species density, cover and diversity varied in relation

to deer presence, with an emphasis on the role of herbivore avoidance in plant community responses to prolonged high levels of herbivory.

MATERIAL & METHODS

STUDY SITE

We studied four islands situated in Laskeek Bay on the East side of Haida Gwaii (British Columbia, Canada): Low, Lost, West Limestone and Haswell (Figure A.1). These islands were located within 17 km of one another and ranged in area from 7.3 to 16 ha (Table A.1). The first two islands have never had deer, the last two islands have had deer for more than 60 years before this study (Vila et al. 2004). On islands colonized by deer, densities were estimated to range from 21 to 37 deer per km² (Stockton et al. 2005).

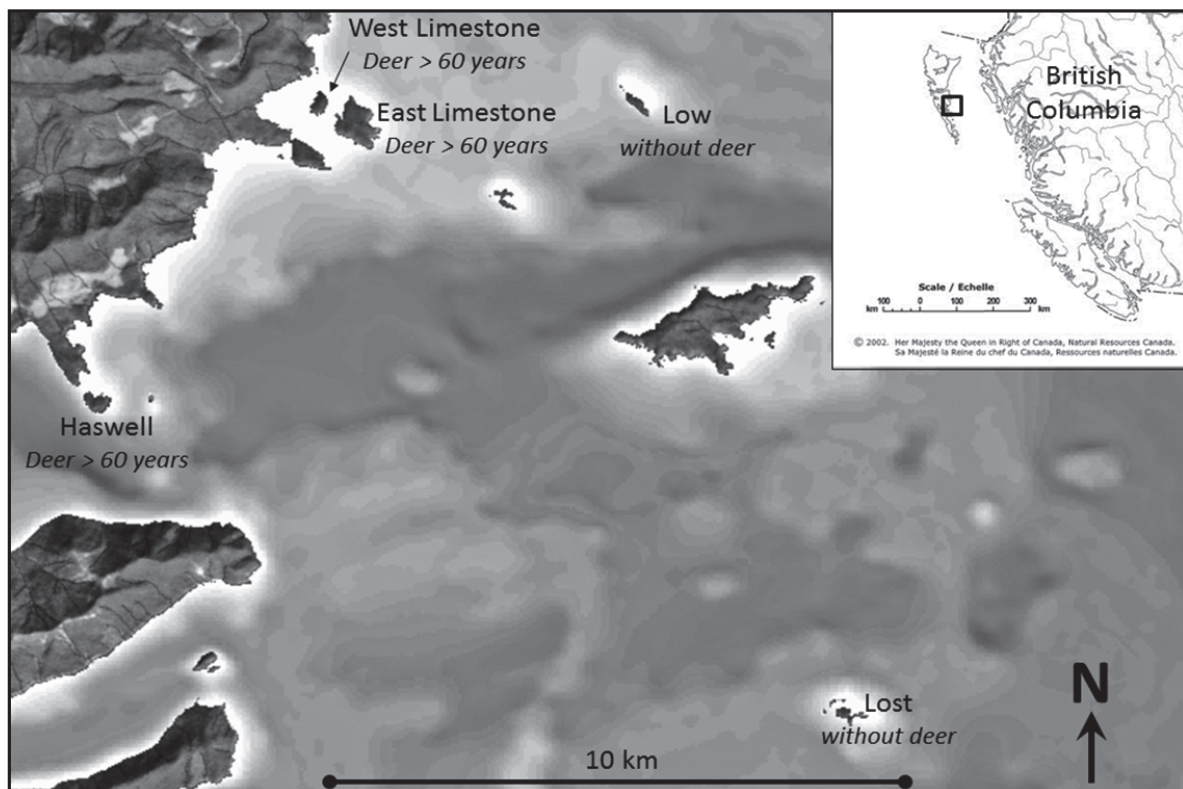


Figure A.1. Study area, showing the position of the 4 study islands used for Bryophytes' surveys and of East Limestone island, the latter used for the foraging study. The length of browsing history (no deer, deer present for at least 60 years) is also indicated for each island. Map courtesy of Gowgaia Institute (<http://www.spruceroots.org/Gowgaia/Gowgaia.html>).

The local forests are part of the coastal temperate rain forest (Alaback & Pojar, 1997) and experience a cool-temperate and humid climate, characterized by year round rainfall. These temperate coniferous forests are dominated by Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*). Due to the geographic isolation from the British Columbia mainland (80 km), the vascular flora of the archipelago is strongly reduced, with only 1/3 of the species present in similar habitats on the mainland (Lomer & Douglas 1999). The bryophyte flora of the islands is nevertheless relatively rich with 575 of the 958 species (60%) described in British Columbia (Golumbia & Bartier 2004).

Table A.1. Island characteristics showing isolation, measured as the distance in meters to one of the main island of the archipelago (Moresby island) and area. Vascular sp. and Bryophyte sp. correspond to the total number of species known on the island. For the vascular plants, data from previous studies have been incorporated (Stockton et al. 2005, Chollet et al. 2013).

Islands	Isolation (m)	Area (ha)	Deer density	Vascular spp.	Bryophyte spp.
Low	5400	9.6	0 deer/km ²	63	19
Lost	7300	7.3	0 deer/km ²	67	15
Haswell	150	13.3	21 deer/km ²	67	12
West Limestone	350	16	37 deer/km ²	59	12

INDIRECT ASSESSMENT OF DEER PREFERENCES

Between June and August 2011 we sampled eleven 10 m² plots (5 m*2 m) on each of the four islands studied (2 without and 2 with deer). Plots were located in the forest interior, at least at 50 m from the forest edge (high-tide line) and 20 m from one another. On islands with deer, we estimated browsing frequencies for the dominant plant species by assessing the proportion of individual plants browsed and not browsed for the species present within the plot. For this we assessed browsing for up to a maximum of 20 randomly selected individuals per species present in a plot. Possible errors in assessment of browsing scars were limited as deer were the only large herbivores present on the islands studied.

DIRECT ASSESSMENT OF DEER BROWSING ON BRYOPHYTES

To directly assess the presence or absence of bryophytes in deer diet, we took advantage of the unusual unwariness of the local deer populations to document their diet by following foraging deer at close range during complete foraging bouts in spring 2009 on East Limestone Island

(Figure A.1). According to Gillingham, Parker and Hanley (1997), complete foraging bouts may be the pertinent observation unit to study foraging behavior and food intake. They defined a foraging bout as a period of time that begins when the first food intake is observed and ends when no food intake is observed for over 2 minutes. Deer diet was quantified by calculating the proportion of time spent browsing different plant species (see Le Saout 2009 for detailed information on the foraging study).

MEASURING COVER OF VASCULAR PLANTS AND BRYOPHYTE SPECIES DENSITY

In each 10 m² plot we visually estimated canopy cover, vascular plant species cover < 4 m (understory, including tree regeneration, shrubs and herbs) and total bryophyte cover. Estimates of percentage cover were made using standard spot-charts (Mueller-Dombois & Ellenberg 1974). The charts provided patterns of black patches corresponding to patch covers of 1%, 5%, 10%, 20% etc. up to 90% respectively.

At each end of the vegetation plots we sampled a 1 m² sub-plot in which we recorded all bryophyte species and their cover to obtain an estimation of the number of species per plot. We identified species in the field for most of them but we collected samples of each for verification in the laboratory. Species were identified with the help of Vitt, Marsh and Bovey (1988) and Flora of North America (1993).

DATA ANALYSIS

The indirect assessment of browsing has been investigated by calculating the percentage of browsed individuals.

For the direct assessment of bryophyte presence in spring deer diet we considered only complete or almost complete foraging bouts. As foraging-bout durations were not equal, they were all pooled together to examine general patterns in deer diet without considering variability in foraging periods among individuals.

Differences in plant cover between islands with and without deer were tested with Wilcoxon tests or Student t-tests depending on normality in data distribution. Bryophyte species density (number of species per plot) and Shannon's index were used to examine species diversity. We

investigated the link among bryophyte cover and vascular understory or canopy using linear regression modeling. All statistical analyses were performed within the R environment (R 2.15.1, R Core Team <http://www.r-project.org/>).

RESULTS

On islands with deer the incidence of browsing of the dominant understory vascular plant was high, ranging from 84% (*Gaultheria shallon*, Table A.2) to 40% (*Tsuga heterophylla*). We observed browsing on only one moss individual and no browsing on liverworts (Table A.2). This lack of consumption of bryophytes by black-tailed deer was confirmed by direct foraging observations at least in spring. During the 85 cumulative hours of foraging surveys we observed no instance of bryophyte consumption by deer (Table A.3).

Table A.2. Browsing frequency of the dominant understory plant species (vascular plants and Bryophytes) assessed in vegetation plots on islands with deer. A maximum of 20 individuals by species were evaluated at each plot leading to a maximum total number of 440 individuals assessed for each species. N refers to the total number of plant individuals assessed for browsing.

Species	N	Growth form	Browsing frequency
Sitka Spruce – <i>Picea sitchensis</i>	183	Tree	60%
Western Hemlock – <i>Tsuga heterophylla</i>	254	Tree	40%
Red Huckleberry – <i>Vaccinium parvifolium</i>	440	Shrub	74%
Salal – <i>Gaultheria shallon</i>	119	Shrub	84%
Red fescue – <i>Festuca rubra</i>	440	Graminoid	50%
Small-flowered Wood-rush – <i>Luzula parviflora</i>	227	Graminoid	46%
Moss spp.	440	Bryophyte	0.2%
Liverwort spp.	288	Bryophyte	0%

Table A.3. Percentage of browsing time spent by foraging deer in spring on different plant groups. Browsing time was assessed by direct observation (see Le Saout 2009 for details).

Plant group	Number of species browsed	Browsing time
Trees	5	48%
Shrubs	2	8%
Forbs	4	2%
Ferns	2	<0.1%
Grasses	5	42%
Bryophytes	0	0%

Bryophyte cover on the forest floor was dramatically higher on islands with deer than on islands without deer (80% and 7% respectively, $p < 0.0001$, Figure A.2). To the contrary, the cover of vascular understory plants was much higher on islands without deer (105%) than in presence of deer (1%, $p < 0.0001$).

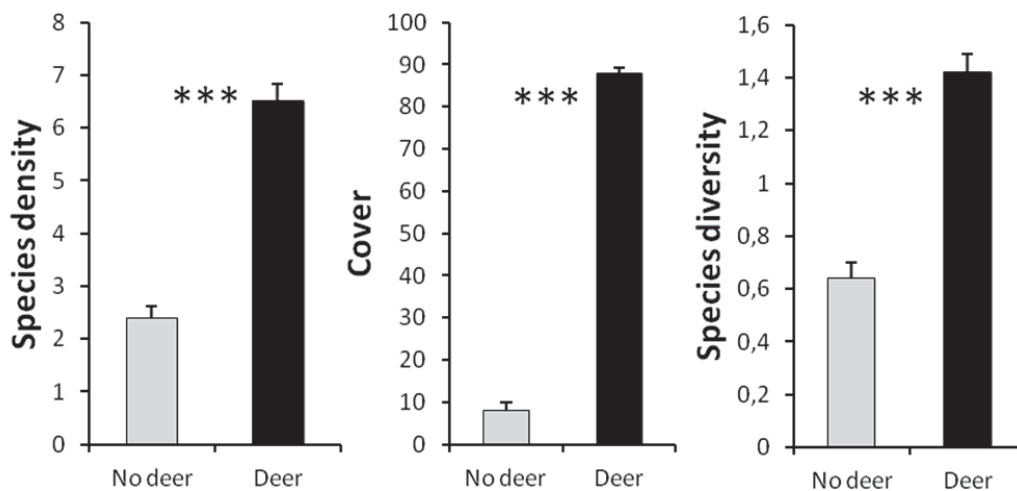


Figure A.2. Species density (number of species per 1 m² plot), percentage cover (%) and species diversity (Shannon's index) of Bryophytes in plots on islands without (gray bar) and with deer (black bar). Stars refer to statistical significance tested by Wilcoxon test (***) < 0.001 .

Linear regression modeling indicated a strong negative relationship between bryophytes and vascular plants ($R^2=0.84$, $p < 0.0001$), but not between bryophytes and canopy cover ($R^2 = 0.01$, $p = 0.44$).

In the bryophyte survey we identified 25 species: 17 mosses and 8 liverworts growing on the forest floor (21 on islands without and 22 on islands with deer, Table A.4). Despite the similarity in the total number of species recorded on the different island categories, the analysis of the 1 m² sub-plots indicated a strong increase in the number of bryophyte species per plot (three times more species per plot), cover (eleven times more) and diversity (Shannon's index twice as high) in the presence of deer (Figure A.2). Analysis by species indicated that 13 of the 25 bryophytes species were more abundant on islands with deer, 11 did not show statistically significant differences, and one species was more abundant on islands that had no deer (Table A.4).

Table A.4. Variation in bryophyte cover (% cover) between islands without (No Deer) and with deer (Deer) in relation to taxonomic group (Tax.) (M = Mosses; L = Liverwort), and tolerance to shade (Shade). Differences were tested by a Wilcoxon test. W = value of Wilcoxon test; p-value and stars correspond to statistical significance tested by Wilcoxon test (*<0.05, **<0.01, *<0.001, ns>0.05).**

	Tax.	Shade	No deer % cover	Deer % cover	W	p-value
<i>Buckiella undulata</i>	M	Tolerant	1.16	7.93	1685.5	P<0.0001***
<i>Dicranum majus</i>	M	Indifferent	0.06	2.22	1188	P<0.0001***
<i>Dicranum scoparium</i>	M	Intolerant	0.04	1.93	1223	P<0.001**
<i>Diplophyllum albicans</i>	L	Tolerant	0	5.04	1518	P<0.0001***
<i>Eurhynchium oreganum</i>	M	Indifferent	1.36	12.32	1585	P<0.0001***
<i>Hylocomium splendens</i>	M	Tolerant	0	12.36	1342	P<0.0001***
<i>Pellia neesiana</i>	L	Tolerant	0.13	1.77	1282	P<0.0001***
<i>Plagiomnium insigne</i>	M	Tolerant	0.02	2.62	1058.5	P<0.05*
<i>Plagiochila porelloides</i>	L	Tolerant	0.04	1.45	1254	P<0.0001***
<i>Pohlia nutans</i>	M	Intolerant	0.02	0.95	1078	P<0.05*
<i>Polytrichastrum alpinum</i>	M	Indifferent	0.02	3.02	1122	P<0.001**
<i>Rhizomnium glabrescens</i>	M	Tolerant	0.32	6.70	1554.5	P<0.0001***
<i>Rhytidiadelphus loreus</i>	M	Tolerant	0.27	25.02	1786	P<0.0001***
<i>Calypogeia azurea</i>	L	Tolerant	0.23	0.57	1010	ns
<i>Calypogeia muelleriana</i>	L	Tolerant	0.004	0	924	ns
<i>Claopodium bolanderi</i>	M	Tolerant	0	0.11	990	ns
<i>Claopodium crispifolium</i>	M	Tolerant	0.34	0	946	ns
<i>Frullania tamarisci</i>	L	Indifferent	0.002	0.5	1013.5	ns
<i>Lepidozia reptans</i>	L	Tolerant	0.5	0.77	987.5	ns
<i>Leucolepis acanthoneuron</i>	M	Tolerant	0.04	0	924	ns
<i>Rhytidiadelphus triquetrus</i>	M	Tolerant	0.93	2.29	938	ns
<i>Scapania bolanderi</i>	L	Tolerant	0	0.07	990	ns
<i>Tortella tortuosa</i>	M	Tolerant	0.008	0.002	946	ns
<i>Ulotia megalospora</i>	M	Tolerant	0.008	0.002	946	ns
<i>Eurhynchium praelongum</i>	M	Indifferent	2.40	0.12	654	P<0.0001***

DISCUSSION

Direct foraging observations in spring and assessment of browsing impact in vegetation plots strongly suggested a year-round lack of bryophyte consumption by introduced black-tailed deer on the islands of Haida Gwaii. This result actually confirms earlier findings in North America and Europe (e.g. McEvoy, Flexen & McAdam 2006; Pellerin, Huot & Côté 2006; Perrin, Mitchell & Kelly 2011). Prins (1982), in his review on bryophyte consumption by vertebrates, indicates that their very low digestibility makes them unattractive to most species. Prins showed that

bryophytes are only a significant component of diets in herbivores living at high latitude such as reindeer - *Rangifer tarandus*, Soay sheep - *Ovis aries*, barnacle goose - *Branta leucopsis*, arctic rodents, for which the high concentration of arachidonic acid in these plants could help fight cold temperatures. Indeed, this fatty acid provides greater pliability for cell membranes at low temperatures, preventing body parts such as food pads from freezing (Prins 1982).

For us, this lack of consumption, the dramatic reduction of understory cover in vascular plants and the sharp increase in bryophyte abundance, species density and diversity we observed on islands colonized by deer are linked. According to Grime's vegetation classification, bryophytes are stress tolerant but are poor competitors (Grime, Rincon & Wickerson 1990; Grime 2007). For example, in the Park Grass Experiment, Virtanen et al. (2000) showed that bryophyte biomass and species richness are negatively correlated with vascular plant cover. Thus the removal of vascular plants in the understory of islands with deer is certainly central in explaining the positive correlation between bryophytes prevalence and effects of overabundant deer. The most likely mechanism is competition for light rather than for nutrients as the growth of bryophyte species is usually more limited by light than nutrient availability (Kull, Aan & Soelsepp 1995; Bergamini & Peintinger 2002). Furthermore, studies on the response of plant communities to increased nutrient availability documented an increase in the cover of grass species that negatively affected bryophytes (Makipaa 1998; Bergamini & Pauli 2001).

Two of the species that are more abundant in presence of deer are actually known to be shade intolerant (*Dicranum scoparium* and *Pohlia nutans*). Of the remaining species that are more abundant in presence of deer, the increased light availability is probably also the main factor explaining the difference in cover between islands with and without deer. However, for two of them, which were totally absent from the samples collected on islands without deer - *Diplophyllum albicans* and *Hylocomium splendens*, an alternative explanation for their higher abundance on islands with deer could be an inability to colonize the islands without deer as these islands are more isolated (Figure A.1). However, this explanation is not consistent with the small size of their spores ($< 20 \mu$, Baldwin & Bradfield 2007) which should allow long-distance dispersal (During 1979).

Among the species that have similar cover on the two types of islands, eight are rare in our dataset, which limits our ability to discuss their response to deer presence (*Calypogeia muelleriana*, *Claopodium bolanderi*, *Claopodium crispifolium*, *Frullania tamarisci*, *Leucolepis acanthoneuron*, *Scapania bolanderi*, *Tortella tortuosa*, *Ulota megalospora*). In the remaining three species, the two liverworts (*Calypogeia azurea* and *Lepidozia reptans*) are not restricted to the forest floor, and also grow on the bark of trees and on woody debris, which are also present on the forest floor of islands without deer (small shrub debris). The third species of this group of species not affected by deer presence, *Rhytidiadelphus triquetrus*, and another species *Eurhynchium praelongum*, which is the only species that is less abundant in presence of deer, belong both to a genus that includes species similar in terms of shade tolerance, habitat preference or dispersal ability but are more abundant in presence of deer. One possible explanation for the decrease of *Eurhynchium praelongum* on islands with deer would be the sensitivity to trampling as has been noted for other bryophyte species (e.g. Arnesen 1999; Ausden et al. 2005; Pellerin, Huot & Côté 2006). Another explanation could be the increase in nutrients that results from the deposition of deer urine and feces. Virtanen et al. (2000) showed that a strong increase in nutrients (N, P and K) reduced the biomass of this species. However, the amount of nutrient added in this experiment was high and results of other studies on the effects of nutrient increase on bryophyte cover and diversity are inconsistent. Responses are positive in some studies (e.g. Ingerpuu, Kull & Vellak 1998; Vanderpuyé, Elvebakk & Nilsen 2002; Armitage et al. 2012) and negative in others (Ingerpuu, Kull & Vellak 1998; Gordon, Wynn & Woodin 2001; Van der Wal, Pearce & Brooker 2005).

The only study that we know of on deer impact on the bryophyte community took place in forest peatlands. The authors found that the white-tailed deer introduced to Anticosti Island (Québec, Canada) had caused changes in species abundance but not in composition (Pellerin, Huot & Côté 2006). In other ecosystems, the response of bryophytes to mammalian herbivory varies among studies. In the case of reindeer, the abundance of bryophytes has been found either to increase (e.g. Vare, Ohtonen, Oksanen 1995; Manseau, Huot & Crete 1996; Olofsson et al. 2001; Pajunen, Virtanen & Roininen 2008) or to decrease (e.g. Olofsson, Moen & Oksanen 2002; Hansen et al. 2007) in response to grazing. Based on these results Van der Wal (2006)

developed one herbivory model in which reindeer grazing elicited a shift from lichen dominated communities to bryophyte dominated communities. If grazing pressure keeps increasing, then these bryophyte dominated communities will further change into communities dominated by grasses (Van der Wall et al. 2004; Van der Wall & Brooker 2004). In the temperate forests we studied this model does not seem to hold. On Haida Gwaii the extreme over-use of vegetation by deer has led to communities dominated by bryophytes and in which grasses were scarce. This difference could stem from differences in selectivity among herbivore species. Reindeer are known to consume bryophytes whereas black-tailed deer do not.

Previous detailed studies on vascular plants on the same islands (Stockton et al. 2005; Chollet et al. 2013) indicated that the large majority of vascular plant species declined in response to deer introduction. Contrary to results from continental studies in situations of overabundant deer (e.g. Horsley, Stout & deCalesta 2003; Rooney 2009), graminoids did not increase on Haida Gwaii in presence of deer. Their abundance decreased but because they were less affected than other species, their relative dominance in these communities increased (particularly in forest edge species, Stockton et al. 2005; Chollet et al. 2013). In fact, browsing frequencies and diet study (Table 2 & Table 3) indicated that graminoids are indeed consumed, but that the low position of their meristem and their high root-to-shoot ratio (McNaughton 1984) provides them better tolerance to herbivory than shrubs, forbs or ferns. Based on our results, we suggest that the increase in graminoid cover that has been observed in mainland studies, usually in presence of more severe winters and higher hunting pressures exerting some control over deer populations, could be a transient phenomenon if the pressure exerted by these deer populations continues to increase.

On Haida Gwaii, where the vegetation has dramatically changed since deer were introduced to the archipelago 150 years ago, reaching the study islands at least 60 years ago, the only group of plants that has increased is bryophytes. In the context of severe herbivory pressure (invasion, overabundance), avoidance seems to confer a particularly important advantage to enable an entire species group to become dominant in a plant community.

Contrary to bryophyte dominated ecosystems (e.g. tundra), where responses of bryophytes to herbivory have been relatively well studied, there is a lack of data in temperate and boreal

forest ecosystems, which limits the possibility of generalization. In the light of our results, we suggest that ecologists pay more attention to this group which plays a key role in ecosystem functioning and has a high conservation profile, particularly in the context of a worldwide trend of increasing *Cervidae* populations.

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Comprendre les fortes densités de cerfs en milieux fortement abrutis: le rôle de la nourriture et de la peur chez le cerf à-queue-noire de Sitka

Les fortes densités actuelles de cerfs causent des problèmes écologiques et socio-économiques. Ces densités restent élevées malgré la forte dégradation des milieux qu'elles occasionnent. Nous explorons les mécanismes qui expliquent ce paradoxe en étudiant les compromis entre disponibilité en ressources et réponses au risque de prédation dans des situations contrastées de nourriture et de risque sur trois îles de Haïda Gwaii (Canada). Les chutes de feuilles de la canopée et la pousse annuelle de plantes rhizomateuses aident au maintien de fortes densités de cerfs. Malgré l'absence de prédation les cerfs maintiennent des comportements de vigilance, réagissent négativement à l'urine de loup, et semblent gérer le risque spatialement plutôt qu'en étant vigilants. Exposés à une chasse expérimentale de basse intensité seuls les cerfs les moins tolérants à la perturbation humaine évitent la zone chassée. Nous discutons les implications de ces résultats pour gérer les populations de cerfs.

Mots-clés : *Ecologie de la peur, Grands Herbivores, Risques de prédation, Ajustements comportementaux et physiologiques, Surabondance.*

Understanding high densities of deer in a heavily browsed habitat: a study on food and fear in Sitka black-tailed deer

In many places deer population have increased in abundance raising serious ecological and socio-economic concerns. Despite the severe degradation deer cause on their own environment, deer seem to remain abundant. How do they do? Predation may have severe impacts on deer behavior and physiology because deer have to trade safety for food. We studied how deer manage food resource and predation risk on three islands of Haida Gwaii (Canada) with contrasted levels of food and risk. We showed that canopy litterfall and the growth of perennial rhizomatous plants help supporting dense deer populations. Predator-naïve deer maintained anti-predation behaviors like vigilance, responded negatively to wolf urine and were likely to manage risk more by space than by vigilance. In response to an experimental low-intensity hunting only the deer the less-tolerant to human disturbance avoided the hunting area. We discussed the long-term effects of hunting as management tool for abundant deer populations.

Key-words: *Fear ecology, Large herbivores, Predation risks, Behavioral and physiological adjustments, Overabundance*