Jeu spatial et interactions comportementales dans la relation prédateur-proie

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Résumé

Prédateurs et proies sont entraînés dans une course spatiale où les prédateurs cherchent à sélectionner les zones du paysage avec une forte disponibilité en proies alors que les proies tentent d'éviter les zones du paysage avec une forte probabilité de rencontrer un prédateur. Ils procèdent incessamment à de nombreux choix susceptibles de modifier l'issue de cette course. Ainsi, en sélectionnant des endroits différents, ils peuvent tenter d'altérer les probabilités de détection, de rencontre ou encore la probabilité de réussite d'une attaque. De nombreuses études empiriques montrent l'importance de l'habitat dans ces choix. On connaît par contre peu les mécanismes de recherche (par les prédateurs) ou d'évitement (par les proies) qui ne seraient pas relatifs à l'habitat. La course spatiale ne résume cependant pas entièrement l'interaction entre prédateurs et proies, laquelle dépend de nombreux comportements non-spatiaux. La vigilance et la socialité des proies constituent des défenses relativement répandues. On a aussi fréquemment observé de nombreux exemples où les proies deviennent actives à un autre moment de la journée pour échapper à leur prédateur. Cependant, on connaît relativement peu les interactions de ces comportements avec la dimension spatiale du jeu proie-prédateur. Dans cette thèse, j'ai pour objectif de combler ces différents manques. Dans le premier chapitre, je propose un modèle théorique montrant l'importance de la prise en compte des comportements spatiaux dans l'interaction classique entre vigilance et taille de groupe chez les proies. Dans le second chapitre, je présente un mécanisme d'évitement des prédateurs par les proies, s'appuyant sur les ancres spatiales et temporelles des prédateurs et ne dépendant pas de l'habitat. Enfin, dans le dernier chapitre, je développe un modèle de choix de parcelles permettant de prévoir comment les connaissances passées sont susceptibles d'être utilisées pour orienter les déplacements. Ce modèle rappelle notamment l'importance de l'imprévisibilité du déplacement dans le jeu prédateur-proie. Ces différents travaux se placent dans le cadre d'une écologie comportementale du paysage et visent à intégrer des mécanismes comportementaux dans l'étude des dynamiques écologiques à l'échelle du paysage.

Abstract

Predators and prey engage into a space race where predators seek to select areas with high prey availability while prey try to avoid areas with a high probability of encountering a predator. Predators and prey continuously make choices that can alter the outcome of this space race. For example, by using different locations in the landscape, they can alter the probability of an encounter, the probabilities of detection or the probability of success of an attack. Many empirical studies show the importance of habitat in these choices. On the other hand, little is known about avoidance by prey or predator search strategies that would be unrelated to habitat. The space race, however, does not fully summarize the interaction between predators and prey, which also depends on many non-spatial behaviors. The vigilance and grouping behaviour of prey are relatively common defenses, and there are many examples where prey become active at another time of day to escape their predator. However, it is still unclear how those behaviors interact with the spatial dimension of the prey-predator game. In this thesis, I will try to fill these gaps. In the first chapter, I propose a theoretical model showing the importance of accounting for spatial behaviors when studying the classical interaction between vigilance and group size in prey. In the second chapter, I present a mechanism of predator avoidance by prey, relying on the spatial and temporal anchors of predators and independent on the habitat. Finally, in the last chapter, I develop a patch selection model to predict how past information should be used to determine movement. This model emphasize the importance of movement unpredictability in the predator-prey game. These different works are part of a behavioral ecology of the landscape and aim to integrate behavioral mechanisms in the study of ecological dynamics at the landscape scale.

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« Trop de questions qui restent sans réponse
Trop de questions et jamais de réponse »
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« Docteur
- Rémi ! »
ou celle là :
« Rémi
- Docteur ! »
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INTRODUCTION

Les stratégies * des prédateurs et des proies

La prédation, une force évolutive.

La prédation est une force importante qui contraint l'abondance et la répartition des proies, tout en façonnant l'évolution des prédateurs et des proies (Dawkins and Krebs 1979; Abrams 2000). Prédateurs et proies montrent de nombreux traits qui contribuent à changer l'issue de leur interaction. Ainsi certains canidés comme les loups (*Canis lupus*), les dholes (*Cuon alpinus*) ou les lycaons (*Lycaon pictus*) disposent de fortes canines et incisives (Van Valkenburgh and Koepfli 1993) et sont capables de se coordonner pour chasser plus efficacement en groupe (MacNulty et al. 2014) : ils peuvent alors attaquer des proies jusqu'à dix fois plus grandes qu'eux (Mech and Boitani 2010; Jędrzejewski et al. 2000; Hayward et al. 2006; Kamler et al. 2012). Pour échapper à la prédation, les jeunes cervidés restent à l'écart de leur mère pendant les premiers jours ou semaines de leur vie (Lent 1974). Ils disposent aussi de traits adaptatifs qui les rendent difficiles à détecter pendant ce laps de temps : ils sont camouflés grâce aux motifs de leur pelage (Stoner et al. 2003; Henderson et al. 2018) et en cas d'alerte ils diminuent leurs rythmes cardiaque et respiratoire pour rester le plus silencieux possible (bradycardie : Espmark and Langvatn 1979 ; apnée : Jacobsen 1979).

Ces deux exemples montrent que les traits des prédateurs et des proies apparaissent à des échelles de temps très diverses sur la durée de vie d'un animal. La dentition et le pelage sont des traits morphologiques qui se mettent en place au cours du développement d'un individu. Ils sont donc relativement permanents, même si les dents peuvent se casser (Van Valkenburgh 1988) ou la coloration du pelage changer au cours du cycle de vie d'un individu (Stoner et al. 2003). À plus courte échelle temporelle on observe les décisions comportementales : les prédateurs peuvent décider ou non de chasser en groupe ; les jeunes cervidés restent immobiles dans un refuge au début de leur vie seulement. Ces décisions comportementales révèlent une grande flexibilité, puisqu'elles sont facilement réversibles. Enfin, l'augmentation du rythme cardiaque d'un prédateur pour s'adapter à un effort physique ou la bradycardie d'un jeune cervidé pour éviter la détection constituent des changements physiologiques pouvant opérer très rapidement, par le biais de réactions nerveuses et hormonales.

Ces différents traits n'interviennent cependant pas de manière isolée, mais toujours en interaction. Pour attaquer des proies massives les canidés utilisent à la fois leurs traits morphologiques (dentition, ossature du crâne) et comportementaux (chasses coopératives). De la même manière, les jeunes cervidés sont plus difficiles à détecter s'ils com-

∗. Dans cette thèse, j'utiliserai parfois le terme 'stratégies' pour désigner les traits des prédateurs et des proies qui sont impliqués dans l'interaction proie-prédateur. Ce terme désignera les traits comportementaux, morphologiques ou physiologiques qui permettent aux proies d'atténuer leur risque de prédation, ou aux prédateurs d'augmenter leur consommation de proies. Le terme de stratégie est utilisé ici sans a priori d'intention de la part des individus. À l'instar de la théorie des jeux, il permet de décrire les options disponibles pour chacun des joueurs, prédateurs et proies. On le préférera à des termes comme les 'défenses' des proies, parce qu'il peut être utilisé de manière symétrique pour le prédateur ou la proie : il évite donc d'adopter préférentiellement le point de vue d'un joueur plutôt que de l'autre

binent leur comportement (rester dans un refuge) avec leur morphologie (pelage cryptique) et leurs réactions physiologiques (bradycardie en cas d'alerte).

La séquence de prédation

Si les traits mis en évidence jusqu'à présent contribuent tous à changer l'issue d'une interaction proie-prédateur, ils ne le font pas de la même manière. Le développement des canines et la chasse coopérative augmentent les chances de réussite d'une attaque sur les proies, mais si les proies sont actuellement plus difficiles à rencontrer qu'à attaquer, le bénéfice de ces traits pourrait s'avérer négligeable. Le camouflage, la bradycardie et l'utilisation de refuges par les jeunes leur permettent de diminuer leur probabilité de détection par les prédateurs mais ils ne changent en rien la probabilité qu'un prédateur ayant détecté un jeune réussisse une attaque. Les traits peuvent en effet intervenir de différentes manières dans l'interaction et pour en comprendre les effets, il faut pouvoir appréhender l'ensemble de l'interaction. En ce sens, Endler (1991) a proposé une suite d'étapes qui constituerait chaque événement de prédation. Pour chaque étape, il présente aussi des exemples de traits des proies – aussi appelés défenses – qui en altèrent l'issue. Ces étapes sont présentées plus bas, ainsi que sur la figure 1, et elles ont été complétées par des exemples de traits des prédateurs affectant les différentes étapes. Ce schéma présente le point de vue du prédateur sur l'interaction et il ne présume pas du moment où les différents traits deviennent actifs, mais uniquement du moment où ils montrent leurs bénéfices. Par exemple le stress physiologique des proies est déclenché au moment où la proie perçoit le prédateur – évènement qui n'est pas présent sur le schéma – alors que les bénéfices d'un métabolisme accéléré sont essentiels plus tard, lorsque le prédateur décide d'attaquer la proie.

La rencontre

Dans la séquence d'Endler (1991), chaque événement de prédation commence par une étape de rencontre (fig.1, étape 1). La rencontre est définie ici comme le moment où une proie se trouve dans le rayon de détection du prédateur. Dans ce contexte, la rencontre ne regarde pas la détection de la proie par le prédateur ou du prédateur par la proie. Il peut donc advenir un événement de rencontre sans que le prédateur ou la proie ne s'en rende compte. Du point de vue d'un prédateur, la probabilité de rencontre va dépendre de la disponibilité des proies dans l'environnement et de sa propre capacité à explorer l'environnement de manière efficace. À Hwange (Zimbabwe), les lions (*Panthera leo*) utilisent de manière plus intensive les zones plus proches des points d'eau (Valeix et al. 2010) lesquelles révèlent une densité de proies plus élevées (Valeix et al. 2009). C'est un exemple de recherche spatialement intensive ('area restricted search' ou 'area concentrated search', Tinbergen et al. 1967 ; Smith 1974) dans lequel le prédateur passe plus de temps dans les zones riches en proies que dans celles avec une densité de proies moins élevée, comme prédit par les théories d'approvisionnement optimal ('optimal foraging', Pyke 1978 ; Benhamou 1992). Formulé autrement, c'est l'exemple d'un prédateur qui sélectionne les zones avec une abondance de proies plus élevée donc une probabilité de

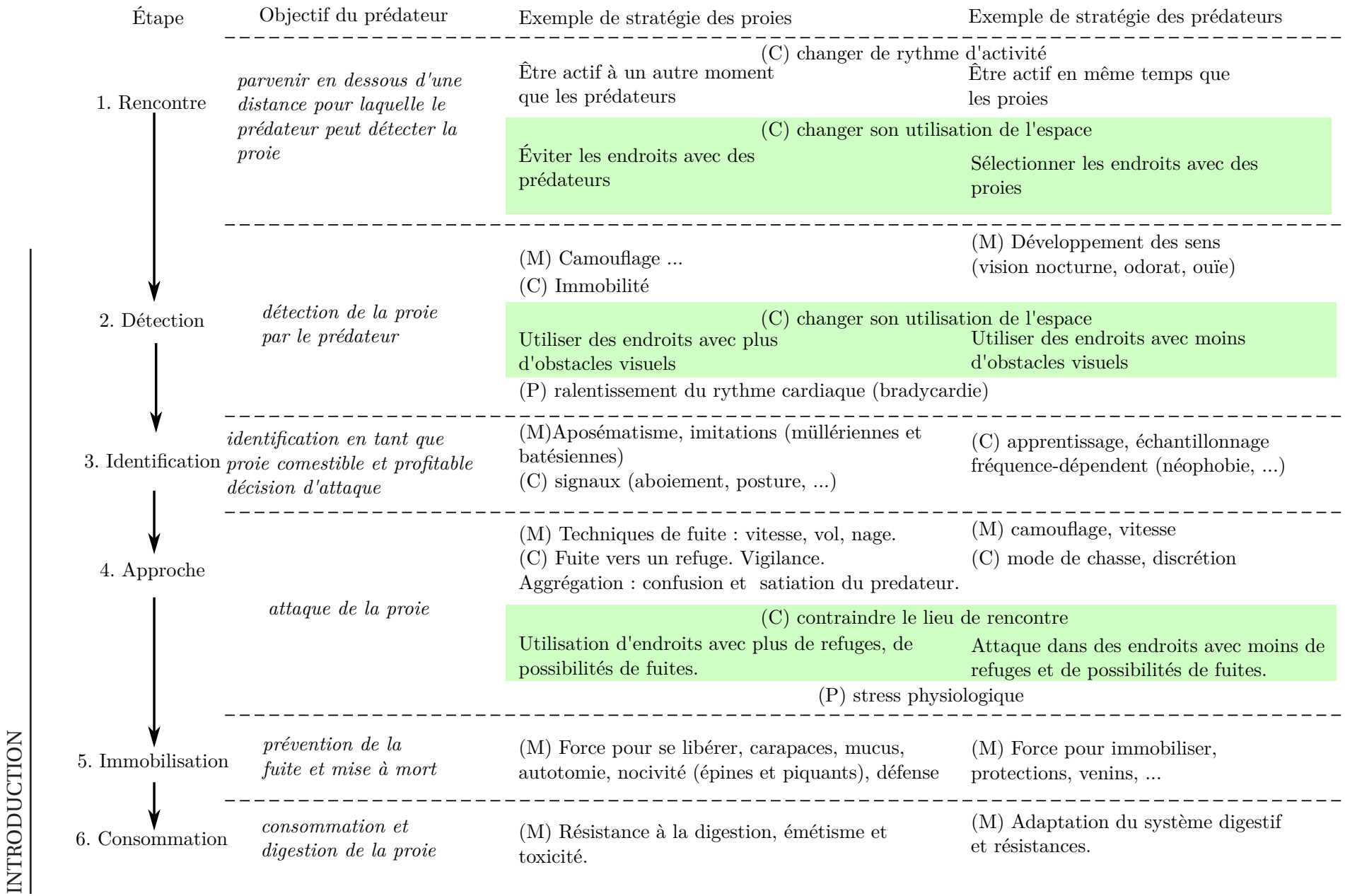


FIGURE 1 – La séquence de prédation, modifiée de (Endler 1991), présente les différentes étapes d'un évènement de prédation, ainsi que les traits des prédateurs et des proies effectifs à chaque étapes. Ces trait peuvent être comportementaux (C), morphologiques (M) ou physiologiques (P). Les comportements spatiaux sont mis en évidence par un ombrage vert.

rencontre fortuite plus forte.

Pour diminuer la probabilité de rencontre fortuite, les proies disposent souvent de stratégies d'évitement qui peuvent être temporelles ou spatiales. Temporellement les proies peuvent diminuer cette probabilité de rencontre en étant actives à des moments différents de ceux du prédateur. Par exemple, sur l'île de Bornéo, en présence de panthères nébuleuses de Bornéo (*Neofelis diardi*), les sangliers à barbe (*Sus barbatus*) deviennent plus actifs la journée et les chevrotains napu (*Tragulus napu*) plus actifs au crépuscule alors que les panthères sont actives la nuit et que dans les zones sans panthères ces deux espèces sont fortement nocturnes (Ross et al. 2013). C'est un exemple d'évitement temporel : en étant actives à des moments de la journée différents, les proies peuvent diminuer leur probabilité de rencontre avec leur prédateur. Spatialement, les proies peuvent diminuer leur probabilité de rencontre avec le prédateur en utilisant préférentiellement les zones avec une probabilité de présence du prédateur plus faible. Ainsi, dans l'écosystème de Hwange (Zimbabwe), les différents brouteurs présents, c'est à dire les girafes (*Giraffa camelopardalis*), les grands koudous (*Tragelaphus strepsiceros*), les céphalophes de Grimm (*Sylvicapra grimmia*) et les raphicères champêtres (*Raphicerus campestris*) sélectionnent les zones où la probabilité de présence d'un des prédateurs principal, le lion, est plus faible à long-terme (Valeix et al. 2009). C'est un exemple d'évitement spatial des prédateurs par les proies.

Bien entendu les prédateurs réagissent aux stratégies d'évitement des proies, puisqu'ils ont eux-mêmes avantage à augmenter leur probabilité de rencontre. Prédateurs et proies sont ainsi engagés dans une course comportementale ('behavioral response race', Sih 1984) qui peut être spatiale (Sih 1998, 2005) ou temporelle (Arias-Del Razo et al. 2011; Monterroso et al. 2013) et dans laquelle les proies cherchent à limiter le chevauchement spatial et temporel avec les prédateurs alors que les prédateurs essaient de le favoriser. Cet aspect sera cependant abordé plus tard.

La détection

Une fois que la proie a été rencontrée, c'est à dire qu'elle est dans le rayon de détection du prédateur, il faut maintenant que ce dernier la détecte : c'est l'étape de détection (fig.1, étape 2). Pour cela, il faut que le prédateur soit capable de discriminer la proie du reste de son environnement, par le biais de ses différents sens (odorat, vision, ouïe) dont le développement peut permettre une détection accrue. Le prédateur peut par exemple augmenter ses chance de détection visuelle des proies si le couvert végétal est relativement limité (Mysterud and Østbye 1999). Il est important de noter qu'une détection accrue de la proie par le prédateur peut aussi limiter ses capacités d'attaque, notamment parce qu'il sera lui même plus facilement détectable, selon les capacités de la proie à le détecter. La présence de couvert peut donc avoir un effet positif ou négatif selon que la détection du prédateur ou de la proie est favorisée (Mysterud and Østbye 1999).

Pour réduire la probabilité d'être détectées par un prédateur, certaines proies utilisent des techniques de camouflage pour se confondre avec leur environnement. C'est le cas des jeunes cervidés que l'on a mentionnés plus haut (Stoner et al. 2003; Henderson et al.

2018) mais aussi de nombreuses autres espèces à travers de nombreux taxons différents : papillons, phasmes, pieuvres, seiches, araignées, caméléons, mammifères, ... (Cott 1940; Stevens and Ruxton 2011). Cependant, le camouflage n'est pas nécessairement visuel, il peut aussi affecter les autres sens (Ruxton 2009). Lorsque les prédateurs détectent plus facilement le mouvement, il peut devenir avantageux pour les proies de diminuer leur activité, voire même de cesser toute activité et de rester immobiles ou à l'abri comme les jeunes cervidés (Lent 1974). Comme précisé plus haut, ces derniers bénéficient aussi d'une diminution du rythme cardiaque lorsqu'ils perçoivent un prédateur, ce qui leur permet de diminuer leur probabilité de détection sonore par le prédateur (Jacobsen 1979).

L'identification et la décision

Une fois la proie détectée par le prédateur, ce dernier doit l'identifier comme étant comestible ou profitable et décider s'il attaque la proie ou non (fig 1, étape 3). Il existe de nombreux travaux sur les stratégies des proies intervenant au cours de cette étape (Caro 2005). Les proies ont en effet intérêt à signaler à leurs prédateurs potentiels qu'elles ne sont pas profitables pour ne pas mourir ou être blessées ni perdre de temps (Leimar et al. 1986). Les prédateurs qui reconnaissent un signal honnête évitent une perte de temps, d'énergie et un risque de blessure ou d'intoxication (Hasson 1991). Ces signaux peuvent être aussi bien morphologiques que comportementaux. Les signaux morphologiques les plus connus sont généralement ceux des proies toxiques qui signalent leur toxicité par une coloration vive, ce que l'on appelle 'aposématisme' (Poulton 1890; Stevens and Ruxton 2011). On retrouve de nombreux exemples d'aposématisme chez les insectes (Motyka et al. 2018) et les amphibiens (Santos et al. 2003; Rudh and Qvarnström 2013). D'autres formes de coloration permettent à la proie potentielle de signaler sa dangerosité et la possibilité pour le prédateur d'être blessé en cas d'attaque. Certains mustélidés comme les blaireaux (*Meles meles*) ou les ratels (*Mellivora capensis*), particulièrement connus pour leur pugnacité, sont rayés de bandes noires et blanches pour signaler cette agressivité (Caro 2009). Par leur comportement, les proies peuvent aussi signaler à leur prédateur qu'elles l'ont détecté, qu'elles sont vigilantes et qu'une attaque aurait des chances de réussite relativement faibles. Par exemple, lorsqu'ils détectent la présence d'un renard roux (*Canis vulpes*), les lièvres d'Europe (*Lepus europaeus*) se tiennent souvent debout sur leurs pattes arrière pour indiquer à leur prédateur qu'ils l'ont repéré, ce dernier met alors fin à son approche (Holley 1993). Les gazelles de Thomson (*Eudorcas thomsonii*) sont quant à elles connues pour approcher et inspecter les guépards (*Acynonyx jubatus*) lorsqu'ils sont à proximité. Ce comportement permettrait à la fois d'indiquer aux guépards qu'ils ont été repérés mais aussi d'informer les autres gazelles de sa présence et favoriserait l'apprentissage des jeunes (FitzGibbon 1994).

Bien sûr, pour que les prédateurs aient intérêt à ne pas attaquer une proie chez laquelle ils identifient un signal, il faut que ce signal soit fiable. Il y a cependant de nombreux exemples pour lesquels l'information des signaux n'est pas complètement fiable. Ainsi en est-il des mimétismes Mullériens et Batésiens. Dans le premier cas, une proie faiblement non-profitable va imiter le signal (la couleur par exemple) d'une proie forte-

ment non-profitable. Dans le second, une proie profitable imite le signal d'une proie non-profitable. Face à l'incertitude de ces signaux, les stratégies d'échantillonnage et d'apprentissage sont critiques pour que la décision d'attaquer effectuée par le prédateur soit bénéfique (Sherratt et al. 2004; Kikuchi and Sherratt 2015). Dans certains cas, il est préférable pour les prédateurs de ne pas échantillonner une proie au signal inconnu et peu fréquent qui pourrait être toxique (Sherratt 2011; Aubier and Sherratt 2015).

L'approche et l'attaque

Une fois que le prédateur a décidé d'attaquer la proie, il doit finalement réaliser l'approche et l'attaque de celle-ci (fig.1, étape 4 ; MacNulty et al. 2014). Cette étape s'arrête lorsque le prédateur entre en contact avec la proie. La réussite de l'approche dépend des capacités de locomotion du prédateur et de la proie, de leurs comportements respectifs (Caro 2005), de l'endroit de la rencontre (Mysterud and Østbye 1999; Gorini et al. 2012), des autres proies présentes (Krause and Ruxton 2002). En ce qui concerne la locomotion, prédateur et proie ont intérêt à aller plus vite que l'autre. Cela se retrouve dans les savanes africaines où les différentes espèces de gazelles, particulièrement sensibles aux prédateurs cursoriaux connus pour leur vitesse comme les guépards, sont aussi parmi les plus rapides (Bro-Jørgensen 2013). Prédateurs et proies peuvent aussi se rattraper ou se distancer en utilisant des moyens de locomotion différents. Certains poissons comme les killis chez les cyprinodontiformes, sont ainsi connus pour être capables de se déplacer sur terre pour échapper à des prédateurs aquatiques (Gibb et al. 2011).

Au moment de la rencontre, les capacités de locomotion sont affectées par le métabolisme de l'individu qui peut changer fortement en réaction à son environnement. En situation de stress comme provoqué par l'attaque d'un prédateur, le prédateur et la proie vont généralement bénéficier d'une activation du métabolisme notamment via une circulation accrue de sucre dans l'organisme. Chez les mammifères, ce circuit est relativement bien connu (Romero, 2004 ; West et al. 2007). Il commence par la stimulation du système nerveux sympathique via l'axe hypothalamo-hypophysaire puis les glandes surrénales. Très rapidement, on observe ensuite une sécrétion massive de catécholamine comme l'adrénaline qui déclenche une augmentation du rythme cardiaque, de la pression artérielle et un afflux sanguin vers les muscles grâce à une vasodilatation importante. En contrepartie, la vasoconstriction du système digestif diminue jusqu'à 90 % de l'afflux sanguin dans les organes viscéraux. Cette nouvelle répartition de la circulation sanguine augmente fortement les capacités locomotrices au détriment des autres fonctions de l'organisme. À plus long terme, la stimulation de l'axe hypothalamo-hypophysaire entraîne une sécrétion de glucocorticoïdes (cortisol, corticostérone) par le cortex surrénal. Ces hormones en circulation dans le sang permettent de mobiliser rapidement de l'énergie : le catabolisme des protéines est activé et libère des acides aminés dans le sang ; les triglycérides des tissus graisseux sont aussi mobilisés pour libérer du glycérol et des acides gras ; finalement la glycémie augmente du fait de la transformation des acides aminés, du glycérol, de l'acide lactique mais aussi de par la diminution d'utilisation du glucose par de nombreuses cellules de l'organisme. Globalement ces changements permettent une

adaptation du métabolisme pour la locomotion, la réparation de tissus en cas de blessure et des dépenses d'énergie importantes.

Au-delà des capacités de locomotion des deux joueurs, le moment où la proie détecte le prédateur peut changer complètement l'issue de l'interaction. Plus tôt le prédateur est détecté, meilleures sont les chances pour la proie de s'échapper. Pour augmenter les chances de détection du prédateur et donc de l'empêcher de réussir son approche, de nombreuses proies montrent des comportements de vigilance (Lima and Bednekoff 1999a; Van Schaik and van Noordwijk 1989) au détriment de l'acquisition de ressources (Cowlishaw et al. 2004; Fortin et al. 2004b).

Lorsque les proies sont grégaires, elles peuvent bénéficier de nombreux avantages (Krause and Ruxton 2002). D'abord la vigilance peut être plus efficace en groupe plutôt qu'individuellement : c'est l'effet de détection (Dehn 1990; Bednekoff and Lima 1998). Ensuite sous réserve que le prédateur ne puisse prélever qu'un nombre limité de proies lors d'une attaque, une proie diminue sa probabilité d'être sélectionnée et donc victime d'une attaque lorsqu'elle est au sein d'un groupe : c'est l'effet de dilution (Lehtonen and Jaatinen 2016). Finalement, les groupes de proies peuvent créer des effets de confusion qui peuvent empêcher un prédateur d'identifier et de suivre un individu (Milinski and Heller 1978; Ohguchi 1981; Krakauer 1995).

Enfin le lieu où se situe l'approche, influencé par l'utilisation de l'espace du prédateur et de la proie, peut tout à fait changer l'issue de l'attaque d'un prédateur sur une proie. En effet, l'habitat du lieu de rencontre peut affecter la détectabilité du prédateur mais aussi comporter une proportion plus ou moins grande de refuges (Mysterud and Østbye 1999; Koivunen et al. 1998; Friedlander and Parrish 1998).

L'immobilisation

Si le prédateur parvient au contact de sa proie, l'attaque est réussie et il doit maintenant l'immobiliser et prévenir sa fuite subséquente (fig.1, étape 5, MacNulty et al. 2014). L'immobilisation dépend du rapport de force entre la proie et le prédateur. Les proies révèlent de nombreuses adaptations destinées à les protéger du prédateur, comme la résistance mécanique des tiques ou la présence de coquilles et de carapaces (Vermeij 1989). Certaines proies (lézards, amphibien) peuvent aussi pratiquer l'autotomie, c'est à dire la section d'une partie de leur corps (ici la queue) saisie par le prédateur pour se libérer (Medel et al. 1988). L'attaque d'un prédateur peut aussi se révéler dangereuse pour celui ci, si les proies sont toxiques (Rudh and Qvarnström 2013; Motyka et al. 2018) ou peuvent le blesser (Caro 2009; Stankowich and Caro 2009).

La consommation/l'ingestion

Finalement le prédateur doit consommer et digérer la proie (fig.1, étape 6). Parfois les proies ont la capacité de ressortir indemnes du système digestif du prédateur (Norton 1988). L'ingestion d'une proie peut cependant se révéler dangereuse pour le prédateur, si la proie n'est pas comestible (Macdonald 1977; Skelhorn and Rowe 2007)

Coûts, compromis et évolution des stratégies

La consommation de la proie par le prédateur n'est réalisée qu'après la réussite des six étapes. Les traits qui permettront à un prédateur de réussir une étape plus facilement ou pour un moindre coût (par ex. temps, énergie) et augmenteront ses chances de survie et de reproduction seront sélectionnés. Quant à la proie, il lui faut interrompre l'interaction avant la réussite de l'étape d'immobilisation (fig. 1, étape 5) pour rester en vie et avoir la possibilité de se reproduire à nouveau. Les traits qui augmentent la probabilité d'une proie de sortir vivante de l'interaction ou dont le coût (par ex. temps, énergie) est moindre seront donc sélectionnés. Par contre, les traits rendant toxiques, émétiques et dangereuses les proies ingérées par le prédateur (fig.1, étape 6) ne seront pas directement sélectionnés puisque les proies les utilisant ne peuvent plus se reproduire. Pour qu'ils soient sélectionnés, il faut que le prédateur cesse d'attaquer les proies possédant ces traits (Leimar et al. 1986).

La sélection des différentes stratégies des prédateurs et des proies ne dépend cependant pas seulement de leur performance dans une seule des étapes ni même uniquement dans l'interaction proie prédateur. En effet certains traits interviennent à plusieurs étapes de la séquences de prédation et pas toujours dans le même sens. Ainsi, l'habitat utilisé par le prédateur et la proie peut conditionner à la fois les probabilités de rencontre, de détection du prédateur et de la proie, ainsi que la vulnérabilité de la proie, généralement, dans des sens différents. En effet, lorsque la proie est plus difficile à détecter pour le prédateur, en cas d'attaque elle a généralement moins de chances de s'en sortir notamment si le prédateur est, lui aussi, plus difficile à détecter. La vie en groupe offre elle aussi un compromis : les proies grégaires bénéficient généralement d'une détection accrue des prédateurs ainsi que du bénéfice d'un effet de dilution (Dehn 1990; Beauchamp and Ruxton 2008; Lehtonen and Jaatinen 2016), mais un grand groupe a aussi potentiellement plus de chance d'être détecté par le prédateur (Aksnes and Utne 1997; Riipi et al. 2001; Hebblewhite and Pletscher 2002) ou sélectionné pour une attaque (Krause and Godin 1995).

Les différentes stratégies qui interviennent au cours de la séquence de prédation et parfois à plusieurs étapes n'ont cependant généralement pas que des effets sur l'interaction proie-prédateur mais aussi sur le reste de l'histoire de vie du prédateur ou de la proie. En effet, les traits morphologiques ont généralement un coût en terme de survie ou de reproduction (Tollrian 1995; Van Buskirk 2000). La sélection prend en compte le compromis entre leurs coûts et leurs bénéfices, c'est à dire leur efficacité à augmenter la valeur sélective de l'individu par leurs effets sur la séquence de prédation. De la même manière les réactions physiologiques et comportementales ont aussi des conséquences négatives sur les autres fonctions de l'organisme. Le stress qui permet une stimulation du métabolisme en cas d'urgence, a des effets négatifs sur l'assimilation de nourriture et la reproduction (Boonstra et al. 1998; Clinchy et al. 2013). La vigilance qui permet de détecter plus facilement les prédateurs, en contrepartie diminue habituellement le taux d'acquisition des ressources (Metcalfe and Furness 1984; Cowlishaw et al. 2004; Fortin et al. 2004b). De manière générale l'évolution des traits qui affectent la séquence de prédation se fait dans le cadre de compromis et on ne s'attend pas à voir des prédateurs, capables d'attaquer

toutes les proies quelles que soient leurs défenses, ni des proies capables de se défendre contre tous les prédateurs (Levins 1968).

Les décisions comportementales dans l'interaction proie-prédateur

Variabilité des stratégies et échelle de temps

Le risque de prédation peut varier fortement au cours de la vie d'un individu, selon son stade de vie (Patin et al. 2015), selon la saison (Jędrzejewski et al. 2002; Sperry et al. 2008; Tolon et al. 2009), ou la présence d'un prédateur dans l'environnement immédiat ou plus lointain (Périquet et al. 2012; Courbin et al. 2016). La disponibilité des proies peut aussi varier spatialement et temporellement (Winder et al. 2001; Giroux et al. 2012; Gervasi et al. 2014). Les traits morphologiques que les proies et prédateurs font évoluer, bien que sélectionnés par la pression de prédation et la nécessité d'alimentation, ne permettent pas de réagir à des changements trop rapides du risque de prédation ou de la disponibilité des proies. Ils sont en effet généralement trop lents et coûteux à développer pour des réactions rapides et temporaires. Les traits physiologiques et comportementaux par contre peuvent tout à fait répondre à des changements beaucoup plus rapides du risque de prédation. Par exemple, lors d'un stress intense causé par la détection d'un prédateur ou d'une proie, il faut 3 à 5 secondes pour que le rythme cardiaque soit doublé et 3 à 5 minutes pour qu'une quantité non-négligeable de glucocorticoïdes circule dans le sang chez les mammifères et oiseaux (Romero 2004; West et al. 2007). S'agissant du comportement, on observe une plus grande vigilance chez les zèbres (*Equus quagga*) lorsque les lions sont présents à proximité, afin de les détecter en cas de tentative d'attaque (Périquet et al. 2012). Ainsi lorsque les lions réussissent une chasse, les autres proies évoluant dans les parages sont généralement informées de leur présence, donc plus vigilantes et par conséquent plus difficiles à attaquer. Face à cette diminution d'une ressource comportementale (la naïveté) qui rend donc les proies moins disponibles (Charnov 1976; Kotler 1992), les lions ont intérêt à se déplacer dans le paysage et à chasser autour d'un autre point d'eau où les proies n'auront pas de réactions comportementales aussi fortes et seront donc plus disponibles (Valeix et al. 2011). Ces ajustements comportementaux et physiologiques sont très rapides et permettent une réaction aux changements que les adaptations morphologiques ne permettent pas (Lima and Dill 1990).

Même si elles peuvent avoir des conséquences importantes à long terme (Boonstra et al. 1998; Clinchy et al. 2013), les adaptations physiologiques interviennent généralement de manière limitée dans la séquence, c'est à dire principalement lors de l'étape d'attaque (fig.1, étape 4). Les stratégies comportementales interviennent quant à elle tout au long de la séquence, principalement jusqu'à la fin de l'étape d'approche (fig.1, étapes 1 à 4) et elles sont aussi les principales causes de changement dans les probabilités de rencontre via l'utilisation de l'espace et les rythmes d'activité. Dans le cadre de cette thèse, je vais donc me focaliser sur les stratégies comportementales, lesquelles permettent de ré-

pondre à des changements de contexte rapides et révèlent une variabilité importante. De plus, je vais simplifier l'analyse d'une interaction proie-prédateur en résumant les étapes d'approche et d'immobilisation (fig. 1, étape 4 et 5) par une simple mesure de la vulnérabilité des proies, c'est à dire la probabilité qu'elles meurent suite à l'attaque du prédateur. On considérera donc que le prédateur a toujours intérêt à attaquer la proie. L'issue d'une interaction sera donc déterminée par (1) la probabilité de rencontre du prédateur et de la proie, (2) la probabilité que le prédateur détecte la proie et (3) la vulnérabilité de la proie.

Le comportement, un outil de gestion du risque de prédation important pour les proies

Comportements proactifs et réactifs des proies

Les réactions des proies au risque de prédation ont été étudiées de longue date (Endler 1991; Caro 2005). On distingue généralement deux types de réactions différentes : proactives et réactives. Les réactions réactives sont déclenchées par un risque immédiat alors que les réactions proactives s'adaptent au risque à long-terme (Creel et al. 2014). La vigilance intense des zèbres en présence de lions, mentionnée plus haut est un exemple de réaction réactive. L'utilisation de refuges par les jeunes cervidés ne dépend pas de la présence immédiate de prédateurs, elle constitue donc une réaction proactive au risque de prédation. Selon le contexte, un même comportement peut être réactif ou proactif. La vigilance peut ainsi être utilisée lorsque le risque est immédiat et qu'un prédateur est dans les parages (Périquet et al. 2012), mais on observe aussi une augmentation de la vigilance dans les milieux risqués par exemple, indépendamment de la présence immédiate d'un prédateur (Dröge et al. 2017).

Le comportement : un médiateur des effets non létaux de la prédation

Si les comportements anti-prédateurs permettent de diminuer certaines composantes du risque de prédation, ils ont généralement aussi un coût en termes de temps ou d'énergie. La vigilance par exemple permet une détection précoce des prédateurs mais en contrepartie elle diminue souvent le taux d'acquisition de ressources (Cowlishaw et al. 2004; Fortin et al. 2004b). Chez les petits passereaux, disposer de réserves de graisses plus faibles en hiver augmente les capacités de vol et donc de fuite en cas d'attaque mais peut aussi augmenter la probabilité de mourir de faim (Metcalfe and Ure 1995; Kullberg et al. 1996; Bonter et al. 2013). Parfois un comportement anti-prédateur à l'égard d'un prédateur spécifique peut augmenter la vulnérabilité vis à vis d'autres prédateurs (Losey and Denno 1998; Eklöv and VanKooten 2001). Ces différents coûts peuvent donc contribuer à limiter la taille de la population de proies et sous-tendent les effets non-létaux du risque de prédation (Werner and Peacor 2003; Preisser et al. 2005). Les effets non létaux du risque de prédation sont les changements de la fitness des proies, de sa dynamique de population ou de la communauté associée qui ne sont pas liés à la consommation de proies par les prédateurs mais causés par les coûts des stratégies anti-prédatrices morphologiques, physiologiques et comportementales (Cresswell 2008). On les distingue des effets létaux

qui sont causés par la consommation des proies et la réduction qui suit du nombre de proies par les prédateurs. L'importance relative des effets létaux et non-létaux n'est pas encore complètement comprise (Creel and Christianson 2008; Schmitz et al. 2017) ; cependant, même si les effets non-létaux sont plus indirects, leurs conséquences peuvent être très importantes (Creel 2011) voire même plus importantes que les effets létaux (Heithaus et al. 2008). Au-delà de l'effet sur la taille des population, les changements de comportement des proies dus à la prédation peuvent aussi avoir des effets en cascade importants sur les autres compartiments de l'écosystème (Schmitz et al. 1997; Trussell et al. 2004; Fortin et al. 2005). Les effets non létaux sont particulièrement visibles lorsque les stratégies par lesquelles ils agissent sont facultatives et dépendent de la présence et de la densité de prédateurs : développement de défenses morphologiques en présence de prédateurs (Tollrian and Harvell 1999), stress en cas de pression de prédation plus importante (Stoks 2001), ajustement de l'utilisation de l'espace et des rythmes circadiens (Ross et al. 2013). Dans ces conditions on peut parfois observer des changements importants dans l'ensemble de la communauté en comparant des zones avec et sans prédateurs ou bien la dynamique d'une zone à la réintroduction d'un prédateur. Les comportements sont généralement des médiateurs importants de ces effets non létaux car leur flexibilité permet de les mobiliser et de ne subir leurs coûts qu'en présence d'un risque de prédation important. Suite à la réintroduction de prédateurs, on observe par exemple de nombreux changements dans l'utilisation des différents types de végétation par les proies, du fait d'une utilisation différentielle des zones par les herbivores en fonction de leur vulnérabilité. Dans le parc national de Yellowstone, la réintroduction des loups a ainsi provoqué une régénération importante des peupliers dans les zones ripariennes, suite à la baisse d'utilisation de ces zones risquées par les wapitis (*Cervus canadensis* ; Fortin et al. 2005). Dans les savanes d'Afrique de l'Est, l'évitement des zones risquées par les impalas (*Aepyceros melampus*) est responsable d'une production fortement diminuée d'épines par les acacias. À l'inverse, dans les zones peu utilisées par les prédateurs (lycaon et léopard, *Panthera pardus*) et donc fortement utilisées par les impalas, les différents acacias disposent de plus d'épines pour se protéger de la pression de l'herbivorie (Ford et al. 2014). Lors d'une translocation d'une aire protégée vers une zone rurale, les thamins (*Cervus eldii*) deviennent nocturnes (Pan et al. 2010) en réaction à la présence humaine diurne, perçue comme un risque de prédation (Frid and Dill 2002). En milieu marin, le risque de prédation par les requins tigres (*Galeocerdo cuvier*) mène les grands herbivores (dugongs, *Dugong dugon* ; tortues, *Chelonia mydas*) à changer leur utilisation des différents habitats, ce qui entraîne un développement différent de la végétation selon le risque du milieu (Burkholder et al. 2013).

Compromis risque/ressources et interaction entre comportements

Les comportements anti-prédateurs peuvent intervenir à plusieurs moments dans la séquence de prédation et parfois dans des sens différents (voir l'utilisation de l'espace, fig.1) et ont presque toujours des coûts, notamment en terme d'acquisition de ressources. Les proies sont donc amenées à faire de nombreux compromis concernant les effets po-

sitifs et négatifs de leurs différents comportements. Si l'investissement dans un comportement anti-prédateur change le contexte dans lequel un autre comportement agit, les investissements dans ces deux comportements pourront être liés. En pratique le compromis le plus fréquent est celui entre le risque de prédation et l'acquisition de ressources (Pettersson and Brönmark 1993; Bonter et al. 2013; Camp et al. 2017; Charalabidis et al. 2017). On a déjà vu l'exemple de la vigilance qui diminue le risque de prédation mais aussi l'acquisition des ressources (Metcalfe and Furness 1984; Fortin et al. 2004b). On observe souvent une diminution de la vigilance lorsque la taille du groupe de la proie considérée augmente (Elgar 1989; Lima 1995; Roberts 1996). Deux théories viennent généralement expliquer cette observation (Dehn 1990). D'abord l'effet de détection suppose que les groupes plus grands sont plus efficaces pour détecter des prédateurs, chaque proie ayant besoin d'être moins vigilante pour avoir la même probabilité de détection du prédateur (Bednekoff and Lima 1998). La deuxième hypothèse, celle de l'effet de dilution, suppose qu'en cas d'attaque un prédateur ne peut prélever qu'une seule proie dans le groupe. Si les attaques ne deviennent pas plus fréquentes lorsque la taille de groupe augmente, chaque individu du groupe verra sa probabilité d'être sélectionné – et donc son risque de prédation – diminuer. À vigilance identique, un individu dans un groupe plus grand subira donc un risque de prédation plus faible (Lehtonen and Jaatinen 2016). Ce constat change le contexte dans lequel l'individu pourra peser les coûts et bénéfices de la vigilance et cela pourra l'amener à diminuer sa vigilance. Ainsi un individu dans un groupe plus grand pourra potentiellement diminuer sa vigilance et bénéficier d'un taux d'acquisition de ressources plus élevé ainsi que d'un risque de prédation plus faible. Ceci dépend bien sûr des formes des relations entre vigilance, taille de groupe et risque de prédation ainsi que de la validité de l'ensemble des hypothèsese (Fortin et al. 2004a; Sirot 2012). D'autres comportements peuvent ainsi faire varier le risque de prédation, comme la distance au couvert. Selon que le couvert puisse servir de refuge pour la proie ou permettre à un prédateur d'être dissimulé, le risque de prédation va diminuer ou augmenter en fonction de la distance au couvert (Mysterud and Østbye 1999). De manière similaire à l'interaction avec la taille de groupe on observe fréquemment des changements de vigilance avec la distance au couvert, dont le sens dépend de la fonction du couvert (refuge ou dissimulation des prédateurs ; Lima 1987; Pöysä 1994; Ebensperger and Hurtado 2005; Beauchamp 2010; Périquet et al. 2010. Ces simples exemples montrent que pour pouvoir appréhender la gestion du compromis risque/ressources par les proies et plus généralement les investissements dans les comportements anti-prédateurs, il faut pouvoir considérer l'ensemble des options comportementales possibles pour les proies.

Approvisionnement optimal et décisions comportementales

Si les stratégies comportementales des proies ont été étudiées de longue date (Lima and Dill 1990; Lima 1998), celles des prédateurs ont été aussi l'objet de beaucoup d'attention, notamment de nombreuses études théoriques sur le comportement optimal des prédateurs. La théorie de l'approvisionnement optimal ('optimal foraging') qui remonte aux années 1960 a été marquée par de nombreux travaux présentant des problèmes d'ac-

quisition de ressources par des prédateurs ou herbivores (MacArthur and Pianka 1966; Schoener 1971; Pyke 1984). Parmi les travaux marquants, le théorème de la valeur marginale ('Marginal value theorem', Charnov 1976) prédit le moment à partir duquel un prédateur doit quitter une parcelle de ressources. Lorsque les ressources d'une parcelle (ici les proies) diminuent au fur et à mesure du temps passé par le prédateur dans la parcelle, ce dernier a intérêt à quitter le patch quand son taux d'acquisition des ressources est inférieur au taux d'acquisition moyen des ressources dans les autres parcelles. Si de nombreux modèles d'approvisionnement optimal ont été étudiés, je vais mettre en avant deux caractéristiques essentielles pour ces modèles : (i) la nécessité de choisir une devise ('currency') et (ii) la spécification des coûts et bénéfices des options disponibles pour le prédateur (Schoener 1971). La devise est la valeur biologique qui doit être optimisée (maximisée ou minimisée). Si les premiers modèles ont étudié la dépression des ressources et sa gestion par les prédateur (Charnov 1976), des développements plus récents ont ajouté la prise en compte par les prédateurs des réactions comportementales des proies. Par exemple, la présence de prédateurs peut rendre les proies plus vigilantes et donc plus difficiles à capturer, créant ainsi une déplétion comportementale des proies (Brown 1999; Mitchell 2009). Ces développements théoriques ont aussi été appliqués aux proies en considérant une ressource végétale, sans réaction comportementale ni mobilité. Dans ce cas la devise à optimiser n'est pas toujours directement la valeur sélective, mais peut être simplifiée par le taux d'acquisition de ressources (à maximiser), un gain énergétique (à maximiser), un temps d'approvisionnement (à minimiser), un ratio du taux d'acquisition des ressources et du risque de prédation (à maximiser) selon la situation (Schoener 1971; Hixon 1982; Kie 1999; Bergman et al. 2001; Kohli et al. 2014). Lorsque la devise d'un modèle prend en compte le risque de prédation des proies, il est possible d'étudier la gestion par les proies du compromis risque/ressources (Lima and Bednekoff 1999b; Bonter et al. 2013). Ces différents modèles d'approvisionnement constituent ainsi une base importante pour l'étude des compromis auxquels font face les prédateurs et les proies.

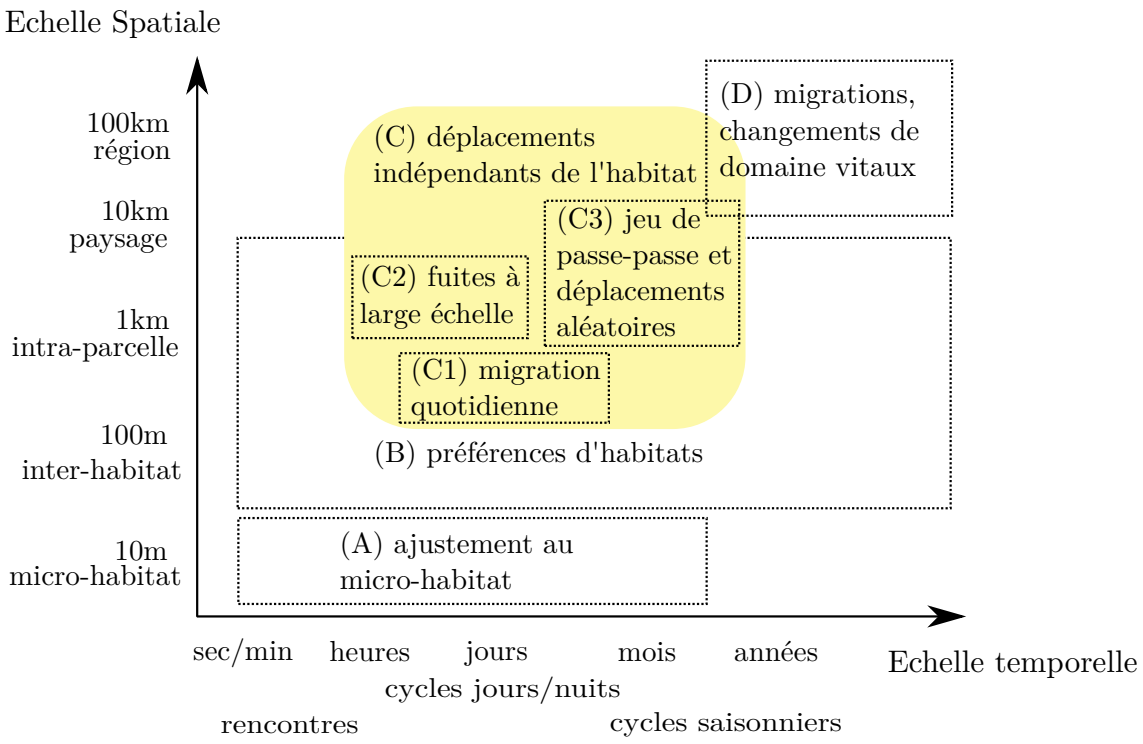
L'importance des comportements spatiaux dans l'interaction prédateur-proie

L'utilisation de l'espace, transversale à la séquence de prédation

Dans le cadre de cette thèse, parmi tous les comportements qui entrent en jeu dans l'interaction entre prédateur et proie, je vais m'attarder sur les comportements spatiaux. Parmi les traits qui interviennent dans la séquence de prédation (Endler 1991, fig1), l'utilisation de l'espace est particulièrement transversale. Elle intervient en effet pour changer l'issue de plusieurs des étapes de la séquence(fig.1, ombrages). Se déplacer offre ainsi de nombreuses opportunités pour altérer les différentes composantes du risque de prédation (voir fig.1). Les densités de proies et de prédateurs qui caractérisent la probabilité de rencontre (fig.1, étape 1), les probabilités de détection (fig. 1, étape 2) et la vulnérabilité (fig. 1, étape 4) sont souvent hétérogènes spatialement (Mysterud and Østbye 1999; Heb-

blewhite et al. 2005; Kauffman et al. 2007; Gorini et al. 2012). Ainsi lorsqu'un prédateur ou une proie se déplace, ils font évoluer leur probabilité de rencontre, de détection ainsi que le taux de succès de l'attaque éventuelle. L'utilisation de l'espace des prédateurs et proies peut donc avoir des effets importants sur les trois composantes du risque de prédation que l'on considère ici : probabilité de rencontre [†], de détection et vulnérabilité.

FIGURE 2 – Stratégies spatiales des prédateurs et des proies.



Importance de l'utilisation de l'espace dans l'interaction proie-prédateur : exemples issus de l'observation

Se déplacer offre donc de nombreuses opportunités pour les prédateurs et les proies. On observe de nombreux cas où l'utilisation de l'espace est au coeur de l'interaction proie-prédateur. En voici maintenant quelques uns, selon l'échelle temporelle et spatiale des comportements (voir fig.2), qui essaient de mettre en avant la diversité des possibilités qu'offre le déplacement pour altérer l'interaction.

(A) À petite échelle spatiale, on observe de nombreux ajustement vis à vis du micro-habitat, comme le couvert végétal dont on a déjà parlé (Mysterud and Østbye 1999; Brown and Kotler 2004) ou la position au sein d'une parcelle ou d'un habitat (Wirsing et al. 2007; Todd and Cowie 1990). Le micro-habitat peut influencer la proba-

†. définie comme dans la séquence de Endler (1991), la rencontre exclut la détection de la proie par le prédateur

bilité de détection des proies, la vulnérabilité en cas d'attaque ainsi que la probabilité de rencontre. Les dugong (*Dugong dugon*) utilisent préférentiellement le bord plutôt que l'intérieur des parcelles d'herbiers lorsque le risque de prédation par les requins tigres est important (Wirsing et al. 2007). Les mésanges bleues (*Parus caeruleus*) préfèrent se nourrir dans les mangeoires proches de la lisière d'une forêt où elles peuvent trouver refuge aisément (Todd and Cowie 1990). Les cerfs mulets (*Odocoileus hemionus*) utilisent préférentiellement certaines forêts, loin de leur lisière (Altendorf et al. 2001). Le micro-habitat peut aussi être un élément critique dans l'utilisation de l'espace des prédateurs. Les lions dépendent par exemple fortement du couvert végétal pour la réussite de leurs attaques (Hopcraft et al. 2005; Davidson et al. 2012). Temporellement, les ajustements par rapport au micro-habitat peuvent être très rapides (Latombe et al. 2014) ou à plus long terme (Jacob and Brown 2000).

(B) L'environnement révèle aussi une diversité d'habitats (Hall et al. 1997; Gorini et al. 2012). Les habitats diffèrent généralement par la disponibilité en ressources pour les proies, l'abondance des proies et des prédateurs ainsi que les probabilités de détection et la vulnérabilité (Hebblewhite et al. 2005; Tobler et al. 2009; Gorini et al. 2012). L'habitat peut varier à très grande échelle spatiale (entre biomes par exemples), mais je vais m'intéresser ici aux variations à l'échelle du paysage, notamment pour laisser de côté les effets confondants qui peuvent l'emporter sur l'effet des différences d'habitat (climats, géographie, ...). Prédateurs et proies montrent de nombreux ajustements aux habitats à des échelles temporelles très diverses (Creel et al. 2005; Kohl et al. 2018; Basille et al. 2013). Lorsque les loups (*Canis lupus*) sont à proximité, les wapitis (*Cervus canadensis*) utilisent plus fortement les milieux forestiers fermés où ils ont moins de chance de rencontrer leur prédateur (Creel et al. 2005). Dans ce cas, les wapitis ajustent leur utilisation des milieux forestiers à quelques heures de l'arrivée et du départ des loups. Ces changements s'observent aussi dans les comportements proactifs à plus long terme, comme on l'a vu plus haut avec l'exemple de la réintroduction des loups au Yellowstone qui a causé des changements dans l'utilisation des habitats ripariens chez les wapitis (Fortin et al. 2005). Il existe aussi beaucoup de cas d'ajustement quotidien de l'utilisation de l'habitat, en réaction au cycle circadien des prédateurs et proies et des variations de vulnérabilité et de détectabilité avec la luminosité (Padié et al. 2015; Kohl et al. 2018). Les cerfs élaphes (*Cervus elaphus*), par exemple, ajustent leur utilisation des différents milieux au cours de la journée (Godvik et al. 2009). Ces variations d'utilisation de l'habitat concernent aussi les prédateurs. Les léopards sélectionnent ainsi les habitats en fonction de la vulnérabilité de leurs proies, au détriment de leur abondance (Balme et al. 2007). Ces différents exemples montrent l'importance de l'habitat comme élément structurant de l'utilisation de l'espace pour les prédateur et les proies.

(C) À plus vaste échelle dans le paysage, les prédateurs (ou les proies) peuvent aussi ajuster leurs déplacements indépendamment de la structure de l'habitat mais en réaction au déplacement de leurs proies (respectivement de leurs prédateur).

(C1) Le risque de prédation varie parfois le temps d'une journée, une des périodes (jour ou nuit) de la journée présentant un risque plus important pour les proies (Fischhoff et al. 2007b; Padié et al. 2015; Kohl et al. 2018). Face à ces variations quotidiennes du risque de prédation, on peut observer des ajustements spatiaux par rapport à la répartition du risque. Ainsi, il arrive que les sangliers se réfugient dans les aires protégées durant la journée, là où la chasse est interdite (Tolon et al. 2009). On observe aussi ces migrations quotidiennes chez les bisons du parc national de Prince-Albert qui fréquentent, la nuit, des zones cultivées à l'extérieur du parc, mais retournent dans le parc durant la journée, pour éviter les risques liés à la présence de l'homme (Fortin et al. 2015). Ces déplacements quotidiens sont bien connus en milieu marin (Alonzo et al. 2003; Hays 2003; Benoit-Bird and Au 2006) même s'ils sont liés à des différences de vulnérabilité plutôt qu'à des changement de distribution et d'activité.

(C2) Après la rencontre avec un prédateur, les proies peuvent montrer des réponses réactives pour atténuer leur risque de prédation. Il existe de nombreux exemples où les proies changent leur utilisation de l'habitat ou leur niveau de vigilance (Creel and Winnie 2005; Périquet et al. 2012; Dröge et al. 2017; Creel et al. 2014), quand le risque immédiat est important, comme après une rencontre. Dans ce contexte, des déplacements à large échelle pour changer de parcelle et éviter ainsi la présence immédiate du prédateur pourraient tout à fait être bénéfique pour les proies. Tel est le cas chez le zèbre des plaines (*Equus quagga*) qui s'éloigne généralement de plusieurs kilomètres -et change de point d'eau- après une rencontre avec les lions (Courbin et al. 2016).

(C3) À plus long terme, prédateurs et proies peuvent tenter de mémoriser les parcelles utilisées par l'autre joueur. Cela a conduit Mitchell and Lima (2002) à proposer le concept de jeu de passe-passe entre le prédateur et ses proies. Dans leur jeu de passe-passe, les proies disposant d'un domaine vital limité tirent du bénéfice à l'utiliser de manière aléatoire plutôt que de concentrer leurs déplacements sur les parcelles ayant le plus de ressources. Ces déplacements aléatoires ne s'avèrent cependant bénéfiques que si les prédateurs sont capables de mémoriser leurs précédentes rencontres (Mitchell 2009).

(D) À très large échelle spatiale et sur une dynamique saisonnière ou interannuelle, prédateurs et proies peuvent recourir à des migrations pouvant modifier leur répartition spatiale et donc leur probabilité de rencontre à très large échelle. La diminution du risque de prédation est d'ailleurs un bénéfice important de la migration pour les proies (Fryxell et al. 1988; Seip 1991; Hebblewhite and Merrill 2007; McKinnon et al. 2010). Les prédateurs peuvent aussi bénéficier d'une disponibilité accrue de proies en migrant (Madsen and Shine 1996; Barnett et al. 2011).

Déplacements, prédation et modèles théoriques

L'importance des réactions spatiales dans l'interaction proie-prédateur a aussi suscité beaucoup d'intérêt et de réflexions théoriques (Fretwell and Lucas 1969; Hugie and Dill 1994; Mitchell and Lima 2002; Flaxman et al. 2011; Merkle et al. 2017; Bracis et al. 2018). Il existe en effet de nombreux travaux sur les choix de parcelles par les prédateurs et les proies (Hammond et al. 2007; Laundré 2010; Flaxman et al. 2011; Merkle et al. 2017) ainsi que sur l'utilisation de l'espace à l'échelle des populations à travers les nombreux modèles de distribution idéale libre (Fretwell and Lucas 1969; Kacelnik et al. 1992; Cressman et al. 2004; Hugie and Dill 1994; Garay et al. 2015). Les modèles de distribution idéale libre ('ideal free distribution', IFD) regardent comment les populations de prédateurs et de proies doivent se distribuer entre les différentes parcelles d'un paysage pour que la valeur sélective des différents individus de chaque catégorie (prédateurs, proies) soit homogène et qu'il n'y ait plus de mouvement entre les différentes parcelles. Parmi les enseignements des IFD, je vais m'attarder sur la notion de course comportementale entre prédateurs et proies (Sih 1984). Les prédateurs ont intérêt à être présents au même endroit que les proies pour augmenter leur probabilité de rencontre alors que les proies cherchent l'inverse. Prédateurs et proies sont ainsi entraînés dans une 'course spatiale' (Sih 1984, 1998, 2005). Pour comprendre qui des prédateurs ou des proies remporte la course spatiale, Sih (2005) propose de s'intéresser aux ancres spatiales des joueurs, c'est à dire leurs contraintes spatiales. Celui du prédateur ou de la proie dont les contraintes spatiales sont les plus importantes devrait être le perdant de la course. Par exemple si les ressources des proies sont fortement hétérogène et concentrées dans des zones restreintes, les proies ont une ancre spatiale importante et les prédateurs et proies vont se concentrer sur ces zones riches en ressources (Bracis et al. 2018). Cette sélection par le prédateur des zones concentrant les ressources des proies, parfois indépendamment de la distribution des proies elles-mêmes est appelée 'effet saute-mouton' (Sih 1998; Flaxman and Lou 2009). Cet effet rappelle un point important de l'interaction proie-prédateur : pour avoir une bonne compréhension de sa dynamique, il est essentiel de considérer à la fois le comportement du prédateur et celui de la proie (Lima 2002).

Objectifs de la thèse

On a vu précédemment l'importance des interactions entre comportements antiprédateurs, telle celle entre la vigilance et la taille de groupe. On a vu aussi l'intérêt stratégique de l'utilisation de l'espace comme outil de gestion du compromis risque/ressources. L'analyse de ces comportements s'est souvent faite de manière distincte. Pourtant de nombreux herbivores se retrouvent face à la possibilité d'utiliser l'ensemble de ces stratégies anti-prédatrices : vigilance, utilisation de l'espace et socialité. On ne sait pas actuellement comment la gestion spatiale du risque de prédation interagit avec les autres comportements anti-prédateurs. Dans le premier chapitre, on proposera donc un modèle théorique de gestion du compromis risque/ressources par des proies sociales pouvant ajuster leur utilisation de l'espace et leur vigilance. Ce chapitre *« Space use*

and leadership modify dilution effects on optimal vigilance under food/safety trade-offs » sera complété d'analyses complémentaires sur le lien entre la taille du groupe et l'utilisation de l'espace chez le zèbre des plaines *« Group-size effect on predation-driven space-use in plain zebra »*.

Il existe de nombreuses études sur le déplacement et ses déterminants, mais jusqu'à présent elles s'intéressaient principalement à la sélection des différents habitats (Fortin et al. 2005; Bastille-Rousseau et al. 2018; Coulon et al. 2008; Van Beest et al. 2012; Gehr et al. 2018). De nombreux travaux ont cependant montré l'importance de la mémoire spatiale (Bailey et al. 1996; Gagliardo et al. 1999; Biro et al. 2007; Mueller and Fagan 2008; Guigueno et al. 2014) et certains travaux récents étudient maintenant son rôle dans le déplacement (Wolf et al. 2009; Oliveira-Santos et al. 2016; Avgar et al. 2015). La prise en compte de la mémoire permet d'introduire de nouveaux mécanismes dans le jeu prédateur-proie et de rappeler l'importance des stratégies d'évitement pour les proies. En effet, si l'habitat peut structurer de manière statique les probabilités de détection et la vulnérabilité des proies, les densités de prédateurs et de proies qui déterminent les probabilités de rencontre ne sont pas une propriété intrinsèque de l'habitat. Si, statistiquement, les propriétés respectives des différents habitats peuvent donner une indication sur les probabilités de rencontres, ces dernières restent potentiellement fortement dynamiques et toute connaissance de leurs dynamiques spatiales et temporelles devraient bénéficier aux prédateurs et aux proies. Si un prédateur ou une proie est capable de prédire le comportement spatio-temporel de l'autre joueur, par exemple grâce à sa mémoire, il pourra en tirer bénéfice. Ceci a deux conséquences :

1. D'abord si le comportement spatio-temporel d'un joueur dépend d'autres caractéristiques que l'habitat, on peut s'attendre à ce que le deuxième joueur présente des déplacements dirigés indépendamment de l'habitat. Les alternances jour/nuit et le cycle circadien fournissent une source de variabilité temporelle qui, modifiant l'activité et potentiellement les déplacements, pourrait donc être à l'origine de déplacements qui ne seraient pas orientés par rapport à un habitat. On connaît l'importance du rythme circadien pour l'utilisation de l'habitat (Godvik et al. 2009; Fischhoff et al. 2007b; Padié et al. 2015; Kohl et al. 2018) . Les milieux marins témoignent aussi d'une forte influence des rythmes circadiens sur le jeu spatial prédateur proie, avec de nombreuses études empiriques et théoriques de migration quotidienne horizontale et verticale (Alonzo et al. 2003; Hays 2003; Benoit-Bird and Au 2006). Si, en milieu marin, ces déplacements sont liés à l'habitat qui se modifie avec la profondeur, ces phénomènes sont avant tout des changements spatio-temporels de densité de prédateurs et de proies auxquels les différents prédateurs et proies de l'écosystème répondent. En milieu terrestre, les migrations quotidiennes décrites sont causées par le risque lié à la chasse (Tolon et al. 2009; Fortin et al. 2015). Ces migrations quotidiennes sont des exemples d'interaction comportementale entre l'utilisation de l'espace et les rythmes d'activité. Je vais présenter un exemple de migration quotidienne dans le second chapitre avec l'exemple du zèbre des plaines (*Equus quagga*). Ce chapitre *« Zebra diel migrations reduce encounter risk with lions at night »* sera complété d'analyses complémentaires sur les comportements anti

prédateurs du zèbre et le cycle circadien - *« La vigilance augmente-t-elle à l'approche du crépuscule ? »* - ainsi que d'un chapitre annexe de méthodologie : *« Identifying stationary phases corresponding to different movement modes or home-range settlements »*.

2. Ensuite, on peut s'attendre à ce que les deux joueurs puissent tirer bénéfice d'un comportement spatio-temporel imprévisible, qui annule toute stratégie se basant sur la prédiction du comportement de l'autre joueur. Des modèles théoriques ont ainsi montré les bénéfices potentiels pour les proies de se déplacer aléatoirement entre les différentes parcelles de leur domaine vital, aussi appelé jeu de passe-passe ('shell same', Mitchell and Lima 2002 ;Mitchell 2009). Si ces modèles ont montré l'importance de la mémoire spatiale des prédateurs dans l'émergence d'un jeu de passe-passe, ils ne permettaient pas aux proies d'utiliser une mémoire spatiale ni une véritable gestion spatiale du compromis risque/ressources. Ces deux aspects des réponses des proies à la prédation sont pourtant relativement bien connus. Les proies ont une mémoire spatiale (Bailey et al. 1996; Mueller and Fagan 2008) qu'elles peuvent potentiellement utiliser en réaction aux expériences passées de rencontre avec des prédateurs (Bracis et al. 2018). Il existe aussi de nombreux exemples d'ajustements spatiaux des proies au compromis risque/ressources (Brown 1999; Sih 2005; Fortin et al. 2005). Un modèle théorique permettant d'aborder ces questions conjointement sera présenté dans le troisième et dernier chapitre intitulé *« Optimal use of past information by enemies in the predator-prey space race »*.

En résumé le plan de la thèse sur articles sera le suivant :

Première partie

DÉPLACEMENTS EN GROUPE ET COMPORTEMENTS ANTI-PRÉDATEURS

Chapitre 1

Space use and leadership modify dilution effects on optimal vigilance under food/safety trade-offs

L'utilisation de l'espace et les décisions de groupe changent les prévisions de l'effet de dilution sur la vigilance optimale dans le cadre d'un compromis entre risque et ressources.

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Abstract

Dilution of predation risk within groups allows individuals to be less vigilant and forage more while still facing lower risk than if they were alone. How group size influences vigilance when individuals can also adjust their space use, and whether this relationship differs among individuals contributing differently to space use decisions, remain unknown. We present a model-based study on how dilution affects the optimal anti-predator behavior of group members, in groups where all individuals determine their vigilance level, while group leaders also determine space use. We showed that optimal vigilance did not always decrease with group size, as it was sometimes favorable for individuals in larger groups to use riskier patches while remaining vigilant. Followers were also generally less vigilant than leaders. Indeed, followers needed to acquire more resources than leaders as only the latter could decide when to go to richer patches. Followers still benefit from dilution of predation risk compared to solitary individuals. For leaders, keeping their leadership status can be more important than incorporating new group members to increase dilution. We demonstrate that risk dilution impacts both optimal vigilance and space use, with fitness reward being tied to a member's ability to influence group space use.

Contents

1 Introduction

Predation risk is an important driver of sociality (Krause and Ruxton 2002). Living in groups generally dilutes predation risk among group members (the so-called 'dilution effect' of grouping; Lehtonen and Jaatinen 2016), and this immediate numerical effect can be complemented by other group-living benefits against predation, such as a collective vigilance that allows for early predator detection (the so-called 'detection effect' of grouping; Dehn 1990, Bednekoff and Lima 1998). As a result, individuals living in groups can benefit from a lower predation risk, which allows them to decrease their own vigilance to increase foraging efficiency. While a decrease in vigilance with increasing group size is commonly reported (Elgar 1989; Lima and Dill 1990; Lima 1995; Roberts 1996; Beauchamp 2013), such relationship is far from being systematically observed. Beauchamp (2008) showed that approximately one-third of the group size – vigilance relationships investigated in bird studies were not significant. The lack of relationship between group size and vigilance is also commonly noted in mammals. This is particularly clear in the taxa with which we have most experience, primates and ungulates. Treves (2000) reviewed some examples in the primate literature, showing that in 9 out of 10 studies on non-human primates no group size effect on vigilance was found. Similarly, many studies on ungulates have failed to found a significant group size - vigilance relationship (e.g. studies on African ungulates: Burger and Gochfeld 1994, Creel et al. 2014; on temperate ungulates: Fortin et al. 2004b). These observations remain puzzling and go against current predictions (Beauchamp 2017). They highlight a gap in our understanding and the need to revisit our theoretical framework for the study of anti-predator behaviors.

Grouping and vigilance are not the only behaviors allowing individuals to respond to predation risk. In particular, individuals also adjust their space use decisions, i.e. their choice of patches or habitats and the time they spent in those, to resource availability and risk levels. Numerous examples exist: baboons (*Papio cynocephalus ursinus*) prefer low quality-low risk to high quality-high risk habitat (Cowlishaw 1997), black-tailed deer (*Odocoilus hemionus*) reduce the time spent near food patches scented with wolf (*Canis lupus*) urine by foregoing feeding (Chamaillé-Jammes et al. 2014), and elk (*Cervus canadensis*) alter their habitat selection when the risk of wolf predation increases (Fortin et al. 2005). These space use decisions influence resource intake and exposure to predators (Brown 1999), which in turn determine the survival of individuals. These decisions are particularly important as prey often navigate in a 'landscape of fear' (sensu Laundré et al. 2001) where predation risk and food resources are not homogeneously spread, and where preys face a trade-off between food availability and safety (Brown and Kotler 2004). This trade-off can emerge from resource depletion in the safest patches initially preferred by the prey, or because richer patches are those where the prey is more vulnerable or more likely to meet a predator. For instance, chacma baboons that forage in the rich riverine vegetation are more vulnerable to leopard or lion attacks that when foraging in poorer patches in the desert region, because of the reduced visibility in the riverine woodlands (Cowlishaw 1997). Such trade-off between food and safety can also emerge if

predator benefits from tracking prey resources rather than prey themselves (Flaxman and Lou 2009). In the boreal forest, wolves select areas with the greatest resources for caribou (*Rangifer tarandus caribou*) and moose (*Alces alces*), thereby creating a food-safety trade-off for these species (Courbin et al. 2014). Therefore, space use decisions are a key component of an individual's anti-predator strategy, and as such, they should be adjusted in interaction with other behaviors such as vigilance and grouping.

The interaction between these three key anti-predator behaviors, grouping, vigilance and space use behavior is not well understood. To the best of our knowledge, no empirical study has investigated in a single study how these three behaviors interact with the others, and only Beauchamp and Ruxton (2007) have provided theoretical insights on this issue. Their model shows that, if individuals can move to a refuge after having acquired sufficient resources, the presence of conspecifics may lead to reduced vigilance. This outcome largely results from the fact that it pays to forage more quickly than other individuals to return to safety earlier, and pass the risk of predation to conspecifics that are still foraging. However, this process occurs less forcefully in large groups because individuals in these groups are less vulnerable to the departure of a single individual. Overall, in the modeled situation, the relation between group size and vigilance could take many forms (increase, decrease, non-monotonic change), depending on parameter values (Beauchamp and Ruxton 2007), demonstrating the potentially strong interaction between patch use, vigilance and group size. In their model, Beauchamp and Ruxton (2007) considered that individuals were non-social and there were no benefits for them to remain within groups after having acquired sufficient resources because they moved to a refuge. The group was simply a temporary aggregation that animals could leave at no cost. Beauchamp and Ruxton's (2007) model would be adequate to study animals that aggregate passively while foraging in suitable areas. The model could for instance be applied to elk that aggregate in open areas at night and return solitarily or in much smaller groups to nearby forest to find cover from wolves (Creel and Winnie 2005). Beauchamp and Ruxton's (2007) model would not apply to social species that form long-term stable associations, in which individuals travel and forage together for long periods. For these species, no theoretical model of anti-predator strategies has yet been formulated.

Strong social cohesion is observed in many species, including some primate (e.g. Van Schaik and Kappeler 1997) and equid (e.g. Rubenstein 1986) species, in which adult group members can stay together for years. It is a striking observation that individuals remain together for long periods of time – and thus use space similarly – even if their needs (given their age, sex, nutritional condition) and vulnerability differ. Much research has been devoted to understand decision-making processes in such groups. Studies have revealed a wide diversity of situations, with decisions about when and where to move ranging on a continuum from being well distributed among group members (i.e. collective/shared decisions) to undistributed (i.e. despotic decisions by a leader) (Bourjade and Sueur 2010; Conradt and Roper 2010; King and Sueur 2011; Strandburg-Peshkin et al. 2015). For instance, detailed studies of the behavior of group members during pre- and post-departure periods in Tonkean macaques (*Macaca tonkeana*) or Przewalski horses (*Equus ferus przewalskii*) have revealed that virtually all individuals can successfully ini-

tiate movements (i.e. decisions are well distributed among group members) and that the actual decisions of moving result from a shared consensus (Bourjade and Sueur 2010). In other species, space use decisions appear much less distributed. For instance, in chacma baboons, the dominant male acts as a despotic leader without coercive behavior, able to successfully lead a group to patches where only it could access the resource (King et al. 2008). Females that have developed social bonds will follow this dominant male because they can benefit from its protective behavior against predators or infanticide by other males (King et al. 2008). Other males will likely follow to maintain their status in the hierarchy, and possibly, for high-ranking males, to obtain some share of the food (King et al. 2008). In vervet monkeys (*Chlorocebus pygerythrus*), older females often lead the group (Lee and Teichroeb 2016). This is also true in harem-forming equid species (Rubenstein 1986), although this may interact with female reproductive status (Fischhoff et al. 2007a). Stallions likely follow to secure the mating opportunities.

Overall, even if some form of collective decision may often exists in stable social groups, in many instances some individuals have much more weight in the movement decision than others. This does not prevent the individuals that contribute less to the decision to remain within the group (Sueur 2012). Accordingly, and irrespectively of our understanding of the processes underlying decision-making and the persistence of stable associations, we note that followers have to cope with space use decisions that they did not influence. When space use decisions determine the risk of predator encounters, differences between leaders and followers in risk perception or in body condition affecting the food-safety trade-off could lead followers to places that are suboptimal relative to their own needs for resource and safety (Sueur and Pelé 2015). In such case, followers can still adjust vigilance levels to deal with the food-safety trade-off. This suggests that vigilance levels and the group size - vigilance relationship could differ among group members, depending on their contribution to space use decisions. These contributions will also likely drive differences in the costs of anti-predator behavioral adjustments (vigilance, space use) across individuals, but this has been overlooked until now and no theoretical predictions exist.

Here we contribute a theoretical study as a first step towards understanding the interaction between group size, vigilance and space use of social species that forage under predation risk and form stable associations in which individuals do not contribute equally to space use decisions. We developed a model to determine optimal vigilance and space use for solitary individuals, and leaders and followers in groups of various sizes. We assumed that increasing vigilance level reduces foraging rate (as observed in primates, e.g. Cowlishaw et al. 2004, and ungulates, e.g. Fortin et al. 2004a), and that individuals forage in an environment made of two patches characterized by a trade-off between resource quantity and predation risk. We used our model to test the following predictions:

(i) for group leaders, we predicted that both optimal vigilance and space use may be affected by a dilution effect, with individuals spending more time in risky places and/or being less vigilant, depending on the relative costs and benefits of predator avoidance and vigilance. Therefore, we also predicted that a dilution effect on optimal vigilance with increasing group size should not always occur when individuals

can also adjust space use to their perception of risk.

(ii) for followers, we predicted that they could decrease their vigilance with increasing group size, but also that this response can depend on the leader's behavior. However, followers face uncertainty about their future foraging opportunities because space use is decided only by leaders; hence, followers may need to forage more to maintain higher energy reserve. The increased foraging effort would come at the expense of vigilance, and we predicted that followers would maintain lower vigilance levels than leaders. Therefore, followers should experience higher predation risk than leaders.

2 Methods

The model is stochastic, and in this article we present the outcome of simulations run with individuals following the optimal behavioral strategies (depending on their leader/follower status, group size and other parameters, see model description and the Results section). These optimal strategies are found using a dynamic programming algorithm (Houston et al. 1988) applied to the model. The dynamic programming procedure is described below in section Finding optimal strategies and running simulations. Model assumptions can be found in table 1, while parameters and equations are summarized in table 2. The model was implemented in Julia (v0.5.12; Bezanson et al. 2015) and the code is available on figshare (Patin et al. 2017).

2.1 Model outline and mathematical formulation

Outline The model uses discrete time steps and simulates the behavior of individuals foraging either solitarily or in groups. Groups are made of a despotic leader, which decides at each time step where the group will forage, and one to seven followers that cannot leave the group. Status – solitary, group leader or follower - is a fixed attribute of individ-

Table 1 – Model assumptions

	Assumption
Groups	- Group size is constant
Predation	- Predator can kill only one prey when encountering a group of prey - Vigilance decreases only the predation risk of the focal individual (no collective detection)
Foraging	- Vigilance and foraging are exclusive - Type II response in foraging - The encounter rate with food items decreases with the time spent vigilant
Optimal Strategy	- Fitness equivalent to long-term survival (non-reproductive season) - Followers know the probability of patch switching, given the patch they currently occupy

Table 2 – Parameters and functional relationships.

Variable	Definition	Formula of value
$v(t)$	Vigilance at time t	$[0-1]$ (21 levels)
$p(t)$	Patch at time t	Risky and rich or safe and poor
$s(t)$	Nutritional state at time t	$[0-40]$ (41 levels)
$c(t)$	Cost: state decrease at time t	$\mathcal{N}(2.5,1,4)$[1]
$g(t)$	Gain : state increase at time t	$\mathcal{N}\Big(\mathrm{G}\big(p(t),v(t)\big),v(t),\mathrm{M}(p)\Big)$[1]
$\mathrm{M}\big(p(t)\big)$	Maximum gain	4 in safe patch, 8 in risky patch
$\mathrm{G}\big(p(t),v(t)\big)$	Mean gain in patch $p(t)$ with vigilance $v(t)$	$\mathrm{A}\times\dfrac{a\big(v(t)\big)\times\mathrm{R}\big(p(t)\big)}{1+a\big(v(t)\big)\times h\times\mathrm{R}\big(p(t)\big)}$
$a\big(v(t)\big)$	Prey encounter rate with food items	$a\big(v(t)\big)=a_0\big(v(t)\big)$
a_0	Prey maximum encounter rate with food items	$a_0=1$
a_1	Cost of vigilance	$a_1=0$ if cost scales linearly with vigilance $a_1=-0.25$ if cost is lower $a_1=0.5$ if cost is higher
h	Handling time	$h=0.75$
$\mathrm{R}\big(p(t)\big)$	Patch resources	$\mathrm{R}(safe)\approx 0.8;\mathrm{R}(risky)\approx 2.54$
A	Duration of a time step	A = 4
$\mathrm{P}red\big(p(t),v(t)\big)$	Probability of being killed by a predator	$k_0\big(v(t)\big)\times\dfrac{1}{\mathrm{N}}\times e^{-k_1 v(t)}$
$k_0\big(p(t)\big)$	Encounter rate with predator	$k_0(safe)=0.001;k_0(risky)\in[0.004,0.008,0.016]$
k_1	Decrease of predation risk with vigilance	$k_1=1.5$
k_2	Increase of encounter rate with group size	$k_2=0$ if there are no increase of encounter rate with group size. $k_2\in[1-8]$ otherwise.
n	Group size	$n\in[1-8]$
$\mathrm{S}tarv\big(s(t)\big)$	Probability of dying by starvation	$1-e^{s(t)f}$
f	Strength of starvation risk	$f\in[0.2,0.25,0.3]$ The larger is f, the smaller the starvation risk

1. $\mathcal{N}(mean,sd,max)$ is for discretized normal distribution of mean $mean$, standard deviation sd and maximum max.

uals. This simple situation (despotic leadership, stable group composition) was used to study the implications of group size and individual contribution to movement decisions on individual vigilance and group space use. The environment is made of two contrasted patches. The likelihood of being attacked is lower in one patch than in the other, but the safe patch is relatively poor in food resources (hereafter defined as safe/poor patch vs. risky/rich patch). No food depletion occurs in the patches. Our model can therefore be thought as representing individuals living at low density and having little impact on the forage basis, compared to others, unaccounted for, factors. Each individual is characterized by a nutritional state s that declines with time if no feeding takes place. An individual's probability of starvation increases with decreasing s, and individuals die immediately if s reaches 0. At each time-step, a decision about where to forage is made by the solitary individual or the group leader. All individuals then decide on their vigilance level. Higher vigilance decreases foraging but increases the chance of surviving an attack. Attacks occur stochastically based on patch-specific, predefined probabilities. When foraging in a group, a given individual is attacked with a probability $\frac{1}{N}$, with N the group size. Thus, individual vigilance level has no impact on the likelihood of being attacked, but it affects the chances of surviving. Note that we focused here on the dilution effect, and we did not include the detection effects that may result from collective vigilance.

Formulation At each time-step:

Computation 1: Solitary individuals and group leaders chose in which patch p(t) to forage, and all individuals decided on their vigilance levels v(t). These state-dependent decisions – the main focus here – were determined during the optimization process. We assumed that individuals had perfect knowledge of the patch characteristics, and that decisions were taken to maximize long-term survival of foragers.

Computation 2: All individuals had their nutritional state s(t) modified: (i) s(t) decreased by c(t), a metabolic cost that was drawn from a discrete normal distribution. The use of a distribution, rather than a set value, introduces some of the natural randomness observed in the energetic costs and gains of individuals, as done by Rands et al. (2003). Technically, a discrete normal distribution is the equivalent of normal distribution for integer values, with the probability of a specific value proportional to the density of the corresponding normal distribution at this value. Here, the discrete approximation of a normal distribution was required by the use of dynamic programming algorithm, which cannot operate on continuous values (Marescot et al. 2013); (ii) s(t) increased by g(t), the amount of resources gained while foraging, drawn from a discrete normal distribution whose parameter depended on patch and vigilance level. g(t) was drawn independently for each individual of a group. In a given patch, the mean amount of resources eaten over each time-step G was assumed to increase asymptotically with local resource biomass, as expected by a type II functional response (Stephens and Krebs 1986), with the resource level of the patch. The en-

counter rate with food items decreases with the time spent vigilant. It follows:

$$\mathrm{G}\big(p(t), v(t)\big) = \mathrm{A} \times \frac{a\big(v(t)\big) \times \mathrm{R}\big(p(t)\big)}{1 + a\big(v(t)\big) \times h \times \mathrm{R}\big(p(t)\big)} \tag{1.1}$$

where

$$a\big(v(t)\big) = a_0\big(v(t)\big) \tag{1.2}$$

with a the encounter rate with food items (equal to a_0 when vigilance $v(t)$ is 0). R(p) is the level of resources in the patch p, h is the handling time, and A is a scaling constant, equivalent to time spent foraging. See fig. A1-A, in Appendix A, for a visual representation of the shape of this function. Note that this formulation of the functional response assumes no interference between individuals.

Computation 3: Individuals may die from predation. The actual presence of a predator in the patch at this time step was determined following a patch-specific, predefined probability k0. This probability was by definition higher in risky patches, and remained constant throughout the simulations. If the predator was present, it always attacked, but could only target one prey. For groups, we assumed that the predator selected the group member to be attacked randomly. Thus, the likelihood of a specific individual being targeted was 1/N. As we focus here on the dilution effect only, we did not integrate the detection effect. We also assumed that the likelihood that an individual died following an attack decreased with its vigilance level, with a diminishing return, as in (Dehn 1990). Specifically, the probability of dying from predation was:

$$\mathrm{P}red(t) = k_0\big(v(t)\big) \times \frac{1}{\mathrm{N}} \times e^{-k_1 v(t)} \tag{1.3}$$

with k_0 the patch-specific predator encounter rate and k_1 a parameter influencing how vigilance affects the likelihood of dying following an attack. See fig. A1-B, in Appendix A, for a visual representation of the shape of this function.

Computation 4: Individuals may die from starvation, with a probability decreasing with its nutritional state s(t), following:

$$\mathrm{S}tar v(t) = e^{-f s(t)} \tag{1.4}$$

with f a parameter influencing how the nutritional state affects the likelihood of dying from starvation. See fig. A2, in Appendix A, for a visual representation of the shape of this function.

2.2 Finding optimal strategies

We determined optimal strategies for space use and vigilance for individuals aiming to maximize their long-term survival using a dynamic programming algorithm (see details in the Appendix B). The dynamic programming algorithm was chosen, because it provided an easy and satisfying way of find prey optimal strategies under simple assumptions (Marescot et al. 2013). More complex assumptions (collective detection for instance) would require a game theoretic approach like genetic algorithm (Ruxton and Beauchamp

2008). Therefore, for solitary individuals and group leaders, we had to find, for any given environment, optimal state-dependent decisions on space use and vigilance. We assumed that individuals optimize their long-term survival which is here a proxy for the fitness. Individual optimal strategies ($p\big(s(t)\big)$ and $v\big((t)\big)$ for the leader and solitary individual, $v\big(s(t), p(t)\big)$ for the follower) are calculated using a dynamic programming algorithm (see e.g. Houston et al. 1988).

For the leader and the solitary individual: J(S, t, T) denotes the probability of survival from day t until day T given that $s(t)$ = S and that the animal follows the best strategy. Maximizing the long-term survival is equivalent to maximize J(S, t, T) with T being very large. We know that:

$$\mathrm{J(S,T,T)} = 1 - \mathrm{P}r_{starvation}(\mathrm{T}|s(\mathrm{T}) = \mathrm{S}) \tag{1.5}$$

$\mathrm{P}r_{starvation}$(T) depends only on S. Therefore J(S, T, T) is known. We also know that :

$$\mathrm{J(S},t,\mathrm{T}) = max_{\pi,\nu}\big(\mathrm{P(S},\pi,\nu,t,\mathrm{T})\big) \tag{1.6}$$

with P(S, π, ν, t, T) the probability that the animal survives untile time T given that he chooses at time t the level of vigilance ν and the patch π. This is known as the stochastic dynamic programming equation. More specifically, with s_{max} the maximum nutritional state:

$$\begin{aligned}\mathrm{P(S},\pi,\nu,t,\mathrm{T}) =& (1 - \mathrm{P}r_{predation}(t|p(t) = \pi, v(t) = \nu)) \\ & \times (1 - \mathrm{P}r_{starvation}(t|s(t) = \mathrm{S})) \\ & \times \sum_{\sigma=0}^{s_{max}} \Big[\mathrm{P}r(s(t+1) = \sigma) \times \mathrm{J}(\sigma, t+1, \mathrm{T})\Big]\end{aligned} \tag{1.7}$$

So J(S, t, T) is the maximum of the different P(S, π, ν, t, T), that we can calculate given that we know J(S, $t+1$, T). The optimal strategy at time t are the corresponding π and ν. As we know J(S, T, T), we can proceed by backward induction and find recursively J(S, t, T) and the associated optimal strategy, i.e. $\pi^*(s)$ and $\nu^*(s)$. Convergence is achieved when the optimal strategy becomes stable over t (see Appendix B, fig. B1 for convergence time).

For the follower : For followers, the optimal vigilance strategy depended on their current nutritional state and on the patch currently used. The optimal strategy of followers thus depended on the sequence of patches used by the leader, but this sequence could not be known in advance because of the stochastic changes of the leader's nutritional status, which in turn influenced its patch use decisions. Thus, finding the optimal strategy for followers required making assumptions on their expectation on space use. We tested two different assumptions about their expectation.

First, we assumed that followers knew the probability of patch switching, given the patch they currently occupied (i.e. that they knew the average residence time in the current patch).

We now need to maximize J(S, π, t, T), the probability of survival from day t until day T given that $s(t)$ = S and $p(t)$ = π. J(S, T, T) is known (as in equation 1.5)and we have :

$$\mathrm{J}(\mathrm{S},\pi,t,\mathrm{T}) = max_{\nu}\big(\mathrm{P}(\mathrm{S},\pi,\nu,t,\mathrm{T})\big) \tag{1.8}$$

with P(S, π, ν, t, T) the probability that the animal survives until time T, given its chosen level of vigilance ν and its currently occupied patch π (imposed by the leader) at time. We have then:

$$\begin{aligned}\mathrm{P}(\mathrm{S},\pi,\nu,t,\mathrm{T}) =& (1-\mathrm{P}r_{predation}(t|p(t)=\pi,v(t)=\nu))\\ &\times(1-\mathrm{P}r_{starvation}(t|s(t)=\mathrm{S}))\\ &\times\sum_{\sigma=0}^{s_{max}}\Big[\mathrm{P}r(p(t+1)=\mathrm{R}isky)\times\mathrm{P}r(s(t+1)=\sigma)\times\mathrm{J}(\sigma,p(t+1)=\mathrm{R}isky,t+1,\mathrm{T})\\ &+\mathrm{P}r(p(t+1)=\mathrm{S}afe)\times\mathrm{P}r(s(t+1)=\sigma)\times\mathrm{J}(\sigma,p(t+1)=\mathrm{S}afe,t+1,\mathrm{T})\Big]\end{aligned} \tag{1.9}$$

To calculate P(S, π, ν, t, T) we have to know the distribution of $p(t+1)$, the patch used at $t+1$ and chosen by the leader. Based on simulation of the leader behaviour we extracted the transition matrix with $p(t+1|p(t))$. This choice assumes that followers know the probability of patch switching, given the patch they currently occupy. Said differently, followers knew what the optimal strategy of the leader was, and have expectations about future space use. See below (Analysis and Results section) for an investigation of the effects of this assumption.

Once we have P(S, π, ν, t, T), maximizing it over ν gives J(S, π, t, T) and the optimal strategy ν(t, S, π). By backward induction with T big enough we can find the optimal strategy ν(S, π).

2.3 Simulations

Once the optimal strategies were found for solitary individuals, group leaders and followers, we simulated their foraging dynamics over time and compared their behavior and overall performance. For each case (solitary, leader, follower) we ran 2000 simulations for distinct individuals (in distinct groups for followers). For leaders and followers, in all simulations, we assumed that group size remained constant, i.e., individuals that died where immediately replaced. Thus, we assumed that the time-scale over which group size could vary was longer than the time-scale over which behavioral strategies were optimal. Strategies were optimized over 250 time-steps but optimal strategies emerged after ca. 50 time-steps. As life expectancy was approximately 150 in the riskier situation modelled, this assumption was verified post-hoc (see details in Appendix B). Individuals started simulations nearby maximum state (Appendix B). During each simulation we recorded patches used, mean vigilance level, mean and standard deviation of the nutritional state, mean probability of dying from predation or starvation (calculated as the average of the instantaneous values from equation 3 and 4), and the total mortality rate. These risks are

presented as probabilities of dying per simulation time-step.

2.4 Analyses

We calculated optimal strategies and ran simulations in three different situations. First, we tested that our model could reproduce the expected patterns emerging from a dilution effect when individuals cannot adjust their space use to deal with the food/safety trade-off, and can only rely on vigilance adjustments. We did so by simulating the optimal behavior of individuals in an environment with only one patch (non-spatial model). In such case, the only anti-predator behavior was vigilance and we expected that it should decrease monotonically with group size. Then, in a two patches context, we explored the different behavioral adjustments to dilution and despotic leadership, by comparing solitary individuals, group leaders and followers. The comparison between solitary individuals and group leaders showed the behavioral adjustments to dilution and their potential benefits. The comparison between leaders and followers informs on how changes in optimal vigilance due to risk dilution were modified by the costs of imposed space use. We assessed how sensitive our conclusions were to changes in the strength of the following determinants of the food/safety trade-off: (i) the level of predation risk, which we modified by increasing risk in the risky patch (see Results section), (ii) the level of starvation risk, which we modified by changing the value of parameter f in equation 4, (iii) the cost of vigilance, which we modified by changing the shape of the relationship between encounter rate with food items and vigilance level. In this last case, equation 2 was modified so that attack rate could vary non-linearly with vigilance, depending on parameter a_1. This gives:

$$a\big(v(t)\big) = a_0\big(1 - v(t)^{1-a_1}\big) \tag{1.10}$$

If $a_1 = 0$, the relationship is linear. If $a < 0$, encounter rate with food items decreases faster than expected under linear assumptions, thereby increasing the cost of vigilance. On the contrary, when $a > 0$, vigilance is less costly. We also investigated how our results were influenced by the fact that the benefits of group dilution can be reduced if larger groups are more frequently encountered by predators, as reported in various predator-prey systems (Krause and Godin 1995; Hebblewhite and Pletscher 2002). Equation 3 was modified to:

$$\mathrm{P}red(t) = k_0\big(v(t)\big) \times \mathrm{N}^{k_2} \times \frac{1}{\mathrm{N}} \times e^{-k_1 v(t)} \tag{1.11}$$

Basal encounter rate with predator k_0 is now multiplied by N^{k_2}. When $k_2 = 0$, the equation simplify into equation (3) and encounter rate does not change with group size. However, when $k_2 > 0$, encounter rate increases with group size. When k_2 is higher, the benefits of risk dilution are reduced because encounter rate with the predator increases with group size. Finally, in a last investigation of the effects of model assumptions, we compared the consequences for the followers to lack knowledge about the long-term patch use of their leaders. For this, we compared the followers' vigilance levels and their predation, starvation and the total mortality rate, under the original model formulation and one

were followers do not have expectation about future patch use and choose, at each time step the vigilance level that maximized their survival to the next time step (i.e. short-term survival).

3 Results

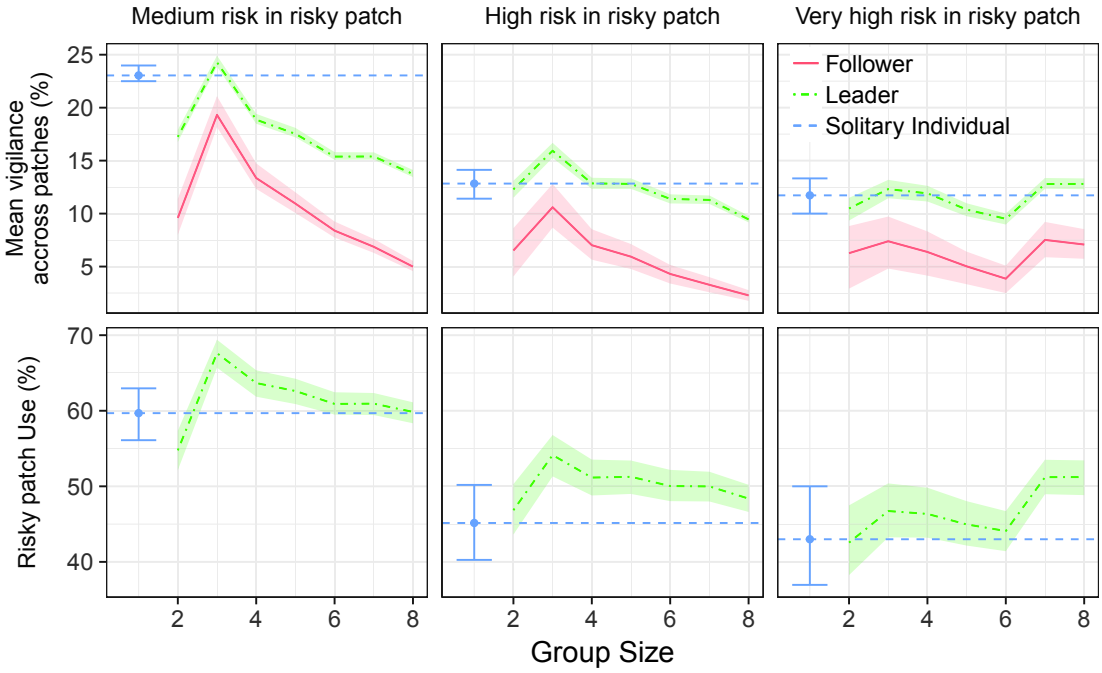

Figure 1 – Relationship between time spent vigilant across patches (%, median, lower and upper quartile, in the upper panel) or time spent in the risky patch (%, lower panel) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch. Patch use is only displayed for leaders because it is identical for followers and their leader. Patterns of how vigilance, averaged across patches (shown here), change with group size, match the patterns observed in the risky patch, because vigilance levels are generally very low in the safe patch (see Supplement 2, fig. S2-1).

3.1 Validating that the model can reproduce expectations about dilution effect on vigilance in the absence of space use decisions

In a model with only one patch where individual took state-dependent decisions about their own vigilance level, the optimal strategies that maximized long-term survival always consisted in increasing vigilance with nutritional state (see Appendix B, fig. B3.). Under different situations, strategies differed in how much vigilance increased. Simulations using optimal behavior showed that, as expected, vigilance declined monotonically with group size (Supplement 1, fig. S1-1), allowing individuals to achieve a higher nutritional state (Supplement 1, fig. S1-2). Accordingly, their risk of dying from starvation

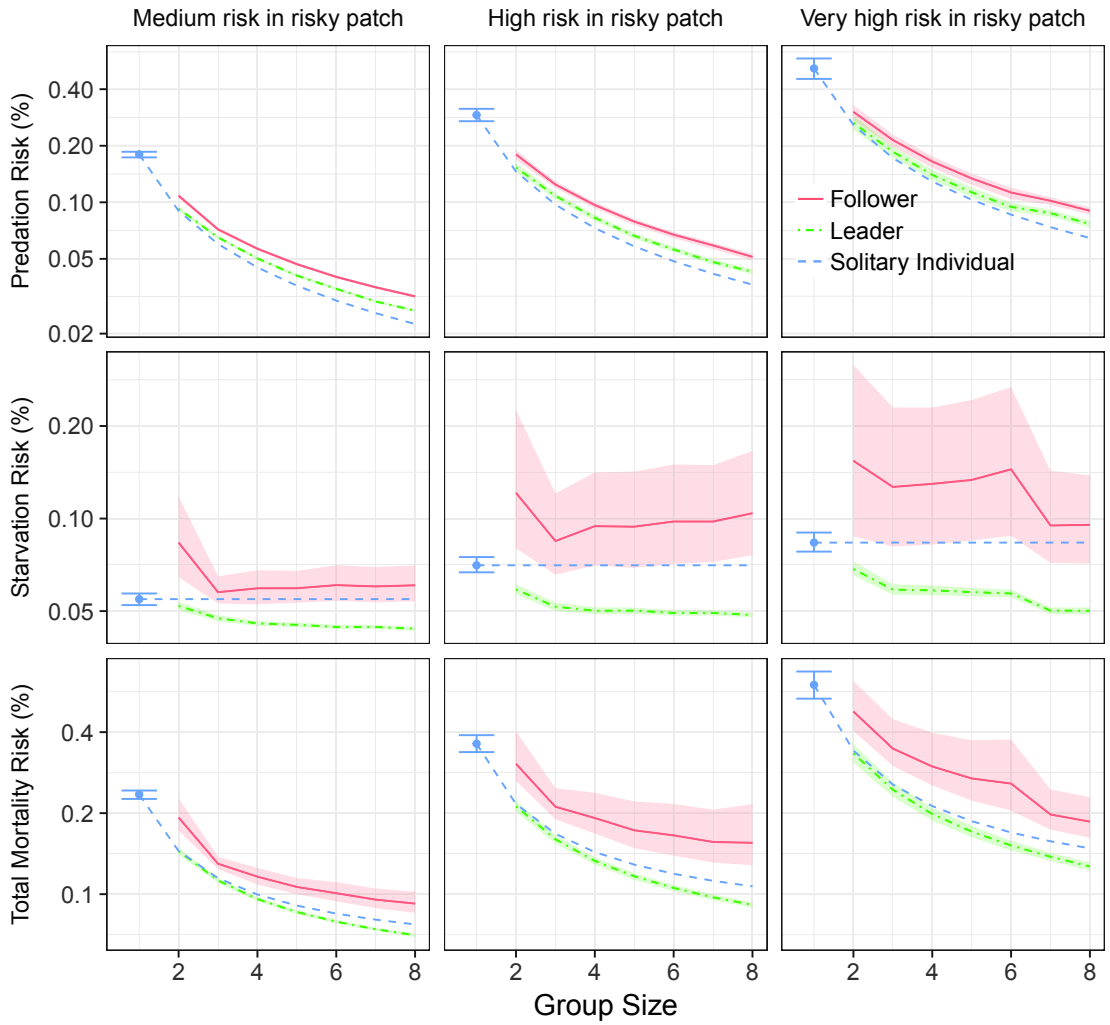

Figure 2 – Relationship between mean experienced predation risk (%, median, lower and upper quartile, in the upper panel), mean experienced starvation risk (%, medium panel) or mean experienced mortality risk (%, lower panel) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch. Dashed lines show risk of a leader that would adopt the optimal behavior of a solitary individual. Percentages correspond to probabilities of death per simulation time step.

decreased with group size (Supplement 1, fig. S1-3, middle panel), concurrently with predation risk, which followed the expected dilution of risk given by 1/N (Supplement 1, fig. S1-3, upper panel). Therefore, we concluded that our model was adequate to study dilution effects and its consequences on the behavior of individuals.

3.2 Optimal state-dependent strategies in a two patch model

For leaders, in a model with two patches, finding the optimal state-dependent strategy consisted in finding in what patch and at what vigilance level should leaders forage, for each possible value of their nutritional state, to maximize long-term survival. We found

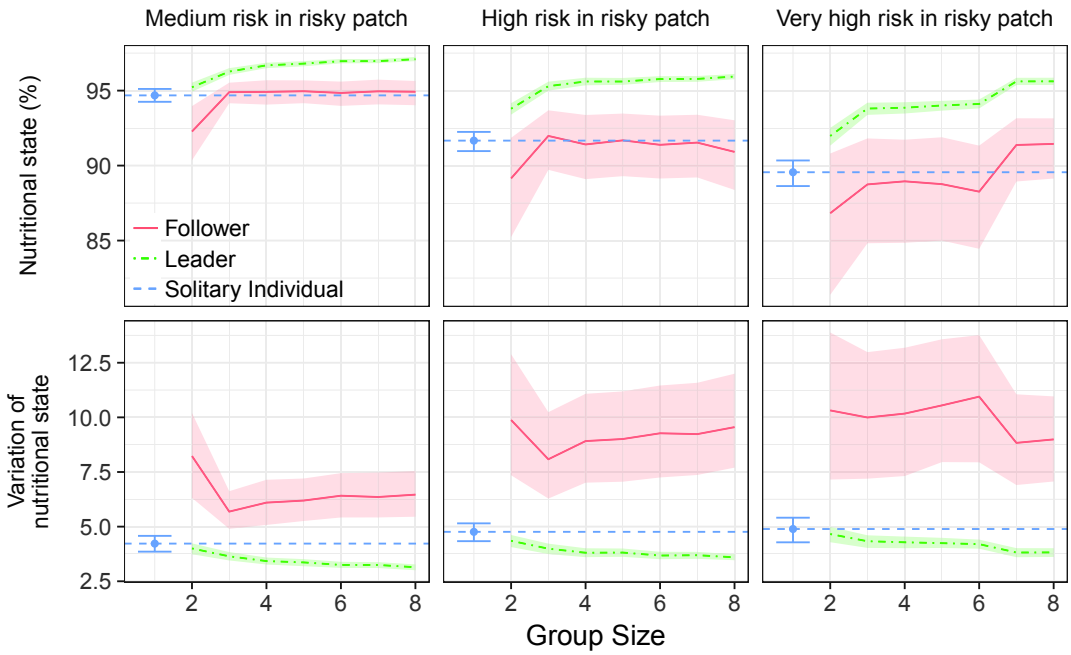

Figure 3 – Relationship between mean nutritional state (% of maximum state, median, lower and upper quartile, in the upper panel) or standard deviation of nutritional state (% of maximum state, lower panel) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch.

that this optimal strategy was, below a certain nutritional state, to forage in the risky patch with no vigilance. As state increased above this nutritional state, the strategy was then to forage in the risky patch with an increasing vigilance level, until the nutritional state reached a threshold value. When the nutritional state was above this value, the optimal strategy made leaders forage in the safe patch at a reduced vigilance level, which however increased as their nutritional state increased to its maximum value. An example of a leader optimal strategy is shown in Appendix B, fig. B4. With different situations of risk level, starvation strength, or other parameters, the strategies differed in the nutritional states at which individuals became vigilant and switched patch, and in the strength of the increase of vigilance with nutritional state, in both the risky and safe patch (not shown). For followers, finding the optimal state-dependent strategy consisted in finding at what vigilance level followers should forage, for each possible value of their nutritional state and for each patch type, to maximize long-term survival. We found that this optimal strategy was, in both patch type, to forage with no vigilance until the nutritional state reached a threshold value, above which vigilance increased with increasing nutritional state. The threshold value at which followers became vigilant was lower in the risky than in the safe patch, in which followers were often always non-vigilant. An example of a follower optimal strategy is shown in Appendix B, fig. B5. With different situations of risk level, starvation strength, or other parameters, the strategies differed in the nutritional states at which individuals became vigilant, and in the strength of the increase of vigilance with nutritional state, in both the risky and safe patch (not shown).

3.3 Consequences of an increase in predation risk in the risky patch

Vigilance and patch use were complementary behaviors to deal with the food/safety trade-off. As risk in the risky patch increased (fig.1 from left to right; see fig. S2-1 in Supplement 2 for patch-specific vigilance), the optimal foraging strategy of solitary individuals or group members shifted from mostly using the risky patch while being highly vigilant to reducing both its use of the risky patch and its vigilance level. Independently of the general level of risk of the risky patch, vigilance and the time spent in the risky patch did not change monotonically or consistently with group size. For example, the optimal space use for groups of three individuals involved a stronger use of the risky patches than groups of two or six individuals, with concomitant changes in overall vigilance levels (fig. 1). Overall, dilution reduced the risk of predation (fig. 2, top panels) and the total mortality risk (fig. 2, bottom panels) of members of larger groups. However, members of larger groups put themselves at greater risk of predation than what would be expected if they were using the optimal vigilance and patch use strategy of a solitary individual while remaining in the group (fig. 2, top panels, dashed line). This management of the food/safety trade-off, and its consequences, however varied strongly between leaders and followers (fig. 2).

These differences are now described. Group leaders were not always less vigilant than solitary individuals because they sometimes increased their use of the risky patch instead (fig. 1). However, they benefited greatly from group living: they had higher and generally less variable nutritional state than solitary individuals, and these differences increased with increasing group size (fig. 3). Accordingly, leaders experienced greater reduction of both starvation risk and predation risk as group size increased (fig. 2).

Followers were consistently less vigilant than solitary individuals, but also less than their group leader (fig. 1). Still, their nutritional state was lower and much more variable than that of their leader (fig. 3). When in smaller groups (2-3 individuals), the nutritional state of followers was sometimes even lower than the one of solitary individuals (fig. 3), indicating that individuals increase their safety at the expense of resource intake when joining a small group with a predetermined leader. The nutritional state of followers increased with group size, but it always remained highly variable (fig. 3), indicating that followers often experienced times of low nutritional state, associated with high starvation risk (fig. 2; see fig. S2-2 in Supplement 2 for an example of such event). Followers had higher predation risk than leaders, but still lower than solitary individuals (fig. 2). Compared to solitary individuals, followers maintained lower vigilance (fig. 1) but experienced lower total mortality risk (fig. 2), demonstrating that the benefit brought by dilution of predation risk within groups exceeds the cost of increased starvation risk.

3.4 Consequences of an increase in starvation risk

Generally, the results presented above hold qualitatively when starvation risk increases. The dilution effect however becomes more beneficial when starvation risk increases (Supplement 3, fig. S3-7, upper panel), as individuals have to be less vigilant to forage more (Supplement 3, fig. S3-1), and changes in vigilance and risky patch use with group size are then more marked (Supplement 3, fig. S3-1 and S3-2).

3.5 Consequences of an increase in the cost of vigilance

Changes in the cost of vigilance mainly changed vigilance levels, but vigilance levels and patch use still varied non-monotonically with group size (Supplement 4, fig. S4-3 and S4-4, left panel). Increasing the cost of vigilance led to lower vigilance levels and lower use of the risky patch (Supplement 4, fig. S4-3 and S4-4, upper panel). When the cost of vigilance was too high, followers were never vigilant and leaders only rarely (Supplement 4, fig. S4-3, upper panel).

3.6 Consequences when a higher group size increases the encounter rate with predator

When group size increased the encounter rate with the predator, the relationships between behavior (vigilance levels, patch use) or predation, starvation, total mortality risks and group size were attenuated (Supplement 4, fig. S4-3 to S4-9, right panel). When the benefit of increased group size became too low, total risk could not be decreased much by trading predation risk against starvation risk (Supplement 4, fig. S4-7 to S4-9, right panel). In such situation, patch use and vigilance of leaders showed a slight monotonic decrease with group size, while risk was not very different compared to a solitary individual. However, followers experienced higher total risk, and they did not benefit anymore from being in a group (Supplement 4, fig. S4-9, right panel).

3.7 Consequences of the lack of knowledge about future space use by followers

If followers had no expectations about future space use, and were to maximize their short-term survival (i.e. their survival until the next time-step), their life expectancy would be really low (Supplement 5, fig. S5-3). With the same nutritional state, followers without expectation about future space use maintained a higher vigilance and thus a lower foraging rate compared to followers with such expectations (compare fig. B4 and B5 in Appendix B). Under situation of short-term maximization of optimal strategy, followers were more vigilant (Supplement 5, fig. S5-1) and had a lower nutritional state (Supplement 5, fig. S5-2/S5-1) than both leaders and followers, with the consequence that they had lower predation risk but higher risk of starvation. Ultimately followers without expectation about future space use experienced a higher risk of mortality. (Supplement 5, fig. S5-3).

4 Discussion

Our study provides, to our knowledge, the first model combining dilution effects of predation risk, vigilance, and space use behavior in heterogeneous environments where a spatial food/safety trade-off exists. This comprehensive model provides multiple explanations, based on optimality principles, for the lack of relationship between vigilance and

group size, or for unexpected forms of this relationship found in many empirical studies (see meta-analysis by Beauchamp 2008). Previous studies have shown that interference within groups and scrounging behavior can alter the relationship between group size and vigilance (Beauchamp 2001, 2003; Fortin et al. 2004b). Here we show that simply considering that individuals can also adjust their space use in response to risk leads to complex relationships between group size, vigilance and space use. The decrease in predation risk from dilution effect can be partially reallocated into resource acquisition either through a decrease in vigilance (and a concomitant increase in foraging) and/or an increase in the use of patches with high predation risk and food availability. Whether individuals will choose to invest more in riskier patch use or to reduce their vigilance depends on the relative efficiency of those two tactics in increasing resource gain while keeping predation risk relatively low. The sudden and erratic changes in vigilance and space use with group size indicate that optimal solutions shift rapidly between riskier space use or decreased vigilance, with increasing risk dilution. Ultimately, we conclude that the lack of a consistent relationship between group size and vigilance levels is not in itself an indication of a lack of dilution effect on behavioral adjustments to predation risk by the prey. Together, and independently of assumptions about leadership, vigilance and space use behaviors offer individuals a wealth of combinations to balance the food/safety trade-off (e.g. Brown 1999, this model). This was already noted by Cowlishaw (1998), who suggested that the lack of group size – vigilance relationship in chacma baboons could be due to the fact that smaller groups spent more time in safer areas and therefore made different vigilance adjustments than larger groups. Cowlishaw (1998) concluded that *"variation in vigilance among individuals may be at least partially attributed to differential investment in other anti-predator behavior"* . Surprisingly, these interactions between anti-predator behaviors remain poorly studied, both empirically and theoretically. Our work is a first step towards reducing this knowledge gap.

Irrespectively of the actual complementarity occurring between vigilance and space use, our results show that dilution consistently allowed group leaders to obtain better and less variable nutritional states than solitary individuals, an advantage leading to lower starvation risk for a similar predation risk. Our results show, however, that followers benefit less than leaders from dilution effect. Although by definition they have the same patch use and thus the same likelihood of being attacked as their leader, followers consistently display lower vigilance. This pattern emerged as a consequence from the followers' inability to adjust space use according to their current nutritional needs. Their optimal strategy anticipates that they will not be able to choose the rich patch when needed to maintain their state. When starvation risk is high, followers face the dilemma of reducing vigilance to increase foraging efficiency, or maintaining vigilance to maintain low predation risk, particularly when the leader has led the group to the risky patch. This anticipation is consistent with Rands et al. (2003)'s model of optimal behavior for pairs of foraging individuals. In their model, individuals with high nutritional state forage when their low-state partner forage, even if their own state is not at stake and if foraging is riskier than resting. This occurs because individuals anticipate that they will need to forage at some point in the near future, and because it is safer to forage when the other forages than when the

other rests (a model assumption). The importance of anticipation is also highlighted by the decreased survival observed when followers' strategies optimize short-term survival, without any knowledge of long-term patch use. Overall, it is clear that optimal foraging strategies in a social context account for the future needs of the individual and for the uncertainty about the behavior of other individuals (timing of foraging in Rands et al. (2003), leader space use decision in our model).

However, our results suggest that in many situations the optimal strategy of followers, leading to reduced vigilance, does not enable them to compensate for the fact that they cannot select food-rich patches – the choice belonging to leaders – when their own nutritional state is low. Indeed, despite the increased foraging resulting from a decrease in vigilance, followers still show a lower nutritional state and thus a higher starvation risk than leaders or solitary individuals. Compared to leaders, the predation risk of followers is also elevated by the reduced vigilance, but it remains much lower than for solitary individuals. Therefore, even if followers do not benefit as much as leaders from dilution effects, the benefits they experience may still be sufficient to promote group formation.

Generally, the differences in benefits brought by grouping between leaders and followers might provide a new explanation for why some individuals may try to prevent the arrival of new members in their group. This rejection of new group members by leaders has been observed in several primates species (Watts 1991; Kahlenberg et al. 2008) and equids (Rubenstein 1986), and has been most commonly attributed to individuals trying to reduce within-group competition. Our model does not include this within-group competition, and increasing group size reduces per capita predation risk. Therefore, immigration of new individuals in the group could be only beneficial, except for the current leader if newly arrived individuals challenge its status. In this case, the leader could benefit from preventing the immigration of new members, to keep his status and enjoy lower starvation and predation risk than followers. For instance, in harem-forming equids (e.g. feral horses, plains zebras - *Equus quagga*), it is generally accepted that foraging competition between members is low (Rubenstein 1994). Addition of a new member to the group should therefore be mostly beneficial to current members as it will reduce their predation risk through the dilution effect. Older females, which generally are group leaders, will however often fight against other females trying to join the group (Rubenstein 1986). Our model suggests that this might be due to the importance of remaining in control of space use decisions. Interestingly, subordinate females are not observed engaging in these agonistic interactions with potential group joiners (Rubenstein 1986). This questions whether a conflict of interest between the leader and followers may exist. Depending on the costs of shifting from being a leader to a follower, and on the relative benefits of increased dilution effect, a leader might want to prevent a potential challenger from joining the group, whereas followers should always benefit from such arrival, in situations where within-group competition is negligible. Such conflicts over acceptance of newcomers between group members of different status has been recently studied in cichlid fish in the context of reproductive dominance (Ligocki et al. 2015), and we call for similar studies focusing on status related to space use leadership.

Like any model, ours provides a simplified representation of real systems based on a

set of assumptions. Two are particularly worth discussing here. First, group size remains fixed. This assumption was made because we were interested in understanding the group size – vigilance relationship, and how group size affects vigilance and space use behaviors. With this in mind, our choice of the dynamic programming optimization algorithm also made it a requirement, and fixed group size was enforced in the model by the immediate replacement of dead individuals. We have shown in Appendix B, section 2, that the algorithm was able to rapidly find the optimal behaviors that maximize the fitness of individuals (vigilance levels in safe and risky patches for followers, vigilance levels in safe and risky patches and time spent in safe and risky patches for leaders), usually well before any individual of the group had died. Thus, the technical need to immediately replace dead individuals occurred only very rarely, and should not have affected our results that can be used to understand optimal vigilance and space use strategies at a given group size. Finally, to study how an individual contribution to space use decisions could affect its vigilance behavior given a specific group size, we used a all or nothing approach by modeling despotic leaders and followers. This simple situation, which may occur but is likely rare in social systems (Petit and Bon 2010; Sueur 2012), allowed us to use a simpler modeling framework, and helped make clear that, in social species forming long-term stable associations, an individual contribution to space use decisions has a strong effect on its vigilance and ultimately its fitness. In systems where leadership is more distributed among group members, i.e. when several individuals can lead the group, such as in horses (Bourjade et al. 2009) or macaques (Sueur and Petit 2010), differences in vigilance and fitness between potential leaders might be reduced. In any case, our work highlights how a currently overlooked process in vigilance studies - the distribution of space use leadership within groups – can create heterogeneity in vigilance among group members.

Conclusion

In summary, using a behavioral model of prey foraging under predation risk, integrating several well-known responses to predation risk – grouping, vigilance and space use – we have shown that expectations on the shape and strength of the vigilance – group size relationship are complex and in particular sensitive to how space use and vigilance affect foraging gains and predation risk. Overall, our results suggest that, although dilution is likely to benefit all group members, the extent of this benefit differs between individuals depending on their contribution to space use decision-making. This emphasizes the need to understand how space use decisions are taken. This is an active field of research, and should allow understanding better how non-consumptive effects of predators affect individuals in social species. However, equally critical is to embrace a multi-behavior perspective when studying anti-predator responses. Individuals can deal with food/safety trade-offs using multiple behaviors, but co-variation and linkages between these behaviors are still poorly studied empirically. This creates a gap between theory and data that must be bridged, possibly thanks to the advances in telemetry that now allow tracking movement, vigilance and social behavior of individuals (baboons: Fehlmann et al. 2017; ungulates: Lynch et al. 2015), and provides an avenue for future fruitful research.

Acknowledgments

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Appendix part A. Summary and discussion of model assumptions

This supplementary section presents :

1. Graphics of the relationships between mean food gain and time spent vigilant, and the probability of dying from predation and time spent vigilant (see figure A1); as well as of the probability of dying from starvation and the nutritional state (figure A2)
2. A short discussion of one specific assumption : vigilance decrease only the predation risk of the focal individual (no collective detection)

Functional relationships underlying the model.

Figure A1 – (A) Relationship between the vigilance level of the individual and its mean resource gain when foraging in the risky (red line) or the safe (blue line) patch, under the default parameter values The amount of resource lost (i.e. metabolic cost) at each time step is also shown (dotted line). Note that an individual cannot survive if it always remains in the safe patch. (B) Relationship between the vigilance level of the individual and its probability of dying from predation when foraging alone in the risky (red line) or the safe (blue line) patch, under the default parameter values (see table 1 in the main text). Probabilities are expressed as per mille.

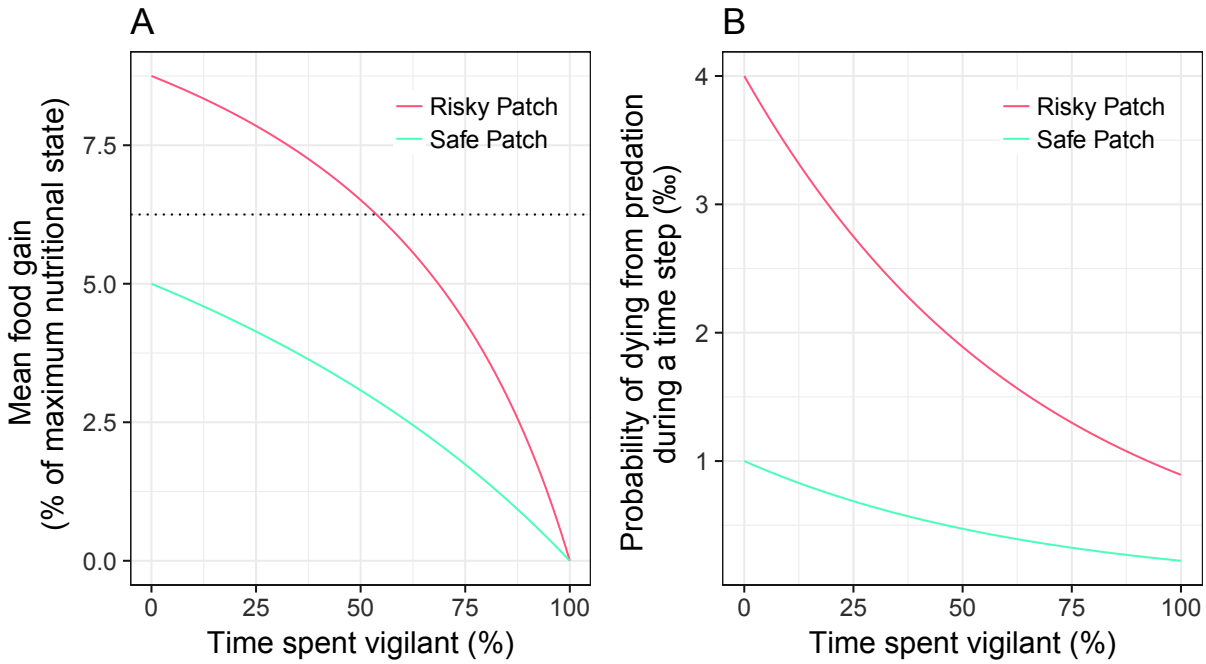
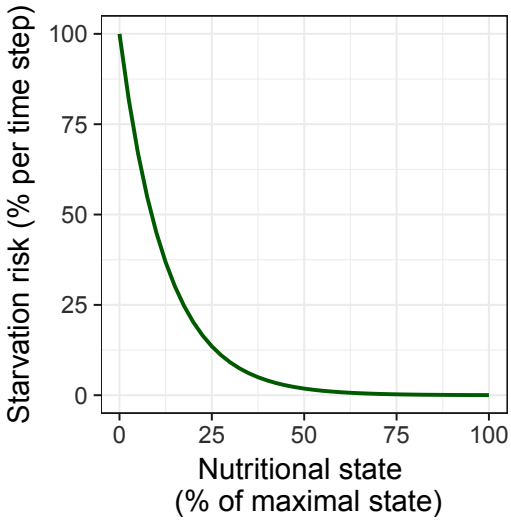


Figure A2 – Relationship between the nutritional state of the individual and its probability of dying from starvation, under the default parameter values (see table 2 in the main text).



Note on the assumption that vigilance decreases only the predation risk of the focal individual.

As our focus was on the dilution effect, we did not model collective detection (also known as detection effect, or 'many eyes effect'; Lima 1995). Collective detection assumes that an individual may benefit from predator detection by other group members. One could test whether or not accounting for collective detection would change the predictions provided by our model. Including collective detection in an optimization framework would require the use of game theory through an evolutionary algorithm (as in Sirot 2012). We do not expect, however, that our results would be affected qualitatively, especially that vigilance and space-use would vary monotonically if one accounted for collective detection. This inclusion should only make groups more efficient at detecting predators. One could argue that followers could rely more than leaders on collective detection, reducing their own vigilance more to minimize foraging costs, thereby reducing the differences in optimal vigilance between leaders and followers in response to predation risk. Collective detection would be beneficial only if predators do not target individuals with lower vigilance levels (Bednekoff and Lima 1998, situation modelled here). Further studies could investigate how relying on group vigilance when state is low could change the effects of group size and leadership on antipredator behaviors.

Appendix part B. Additional information on optimal strategies; convergence and examples; and initial nutritional state in simulations

This supplementary section presents :

1. a check of the convergence of the dynamic programming algorithm and a comparison with the resulting life-expectancy.
2. examples of optimal strategies for individuals using a single patch (fig. B3), leaders (fig. B4), followers (fig. B5) and followers without knowledge of long-term patch use (fig. B6) using two patches.
3. information on the choice of the initial nutrtional state for individuals in the simulation.

Check of convergence and comparison with life expectancy

Calculations of optimal strategies using the dynamic algorithm were made on 250 time-steps. We used the last change in the calculated strategies as the convergence time. As we see on figure B1, strategies stopped changing after 20 to 40 time-steps in most cases and after 100 time-steps for the longest cases, still far from the 250 time-steps of the algorithm. We can therefore conclude that the dynamic programming algorithm has converged.

We compared these convergence time to the resulting life expectancy of these strategies (see figure B2 for the life expectancies). Life expectancy for individuals in a group were most of the time higher than 200 time-steps. This shows that strategies are optimal on a shorter time scale than the time scale on which group size might change if individuals were to die without being replaced. In the riskier cases (small group size and very high risk in the risky patch), those time-scales are closer, as follower vigilance in the risky patch converges around step 100 and life expectancy is slightly higher than 100 time-steps. However the strategies at convergence are very close to the strategies at step 70 (less than two changes in vigilance level).

Figure B1 – Relationship between the number of time steps required for convergence of the optimal strategy and group size, for follower vigilance in safe (green) and risky patch (red), leader vigilance (blue) and patch use (purple), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch.

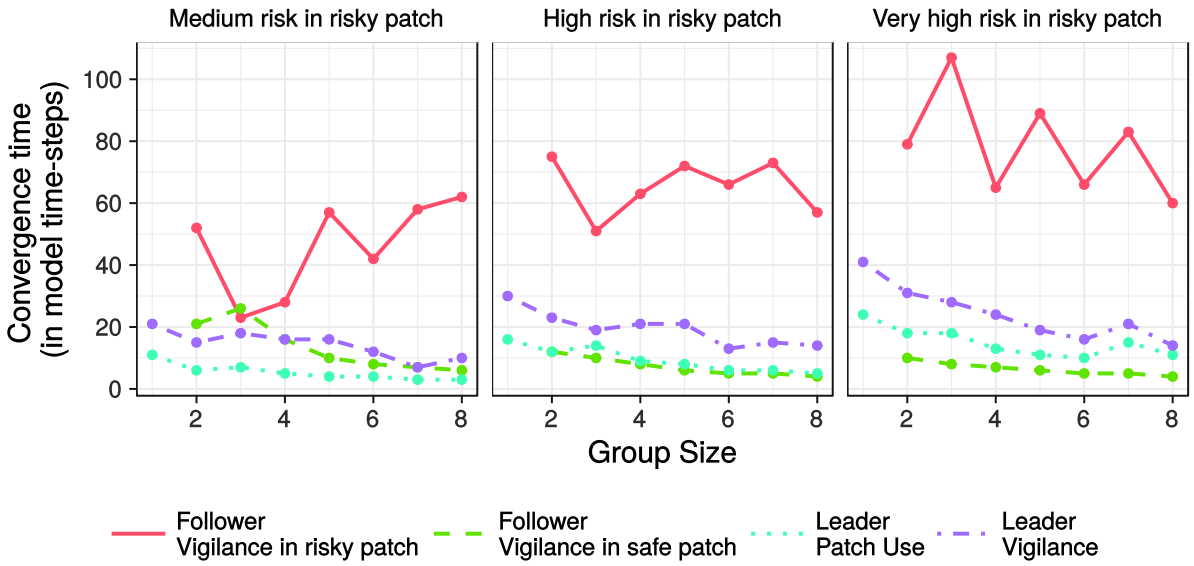
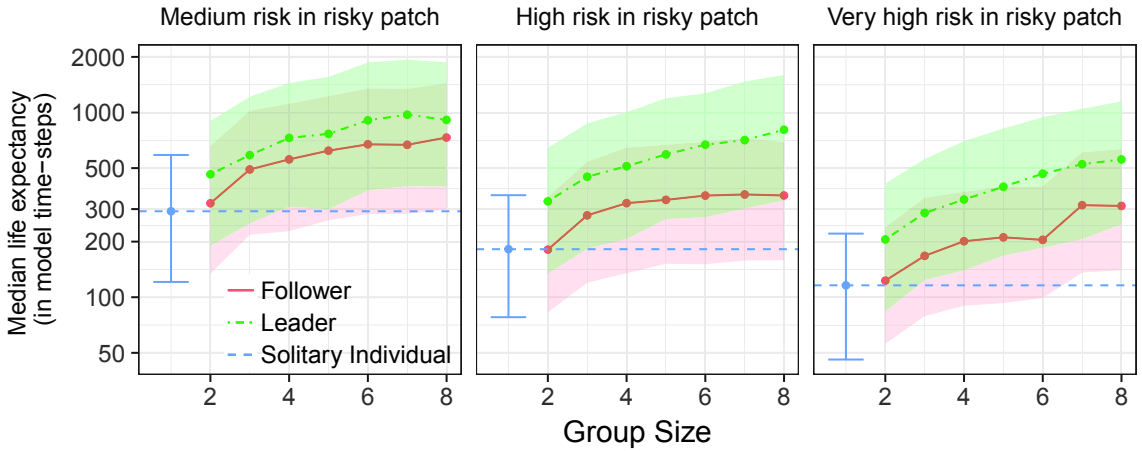


Figure B2 – Relationship between life expectancy (in model time steps, median, lower and upper quartile, in the upper panel) and group size for leader (green), solitary individual (blue) or follower (red) in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch.



Examples of optimal strategies

Figure B3 – Optimal choice of vigilance given the nutritional state of an individual in a group of 2 individuals using only one patch. $k_0(risky) = 0.004$, $f = 0.2$, $k_2 = 0$, $a_2 = 0$.

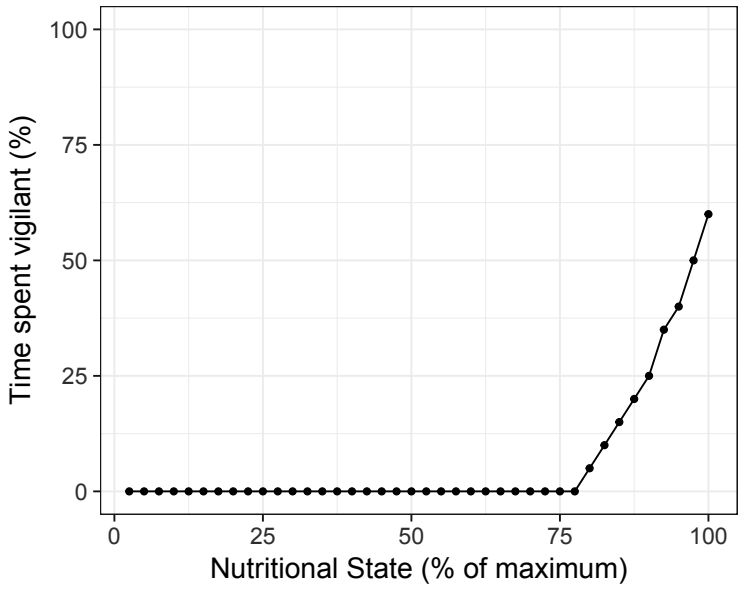


Figure B4 – Optimal choice of vigilance and patch given the nutritional state of a leader in a group of 2 individuals. $f = 0.2$, $k_0(risky) = 0.004$, $k_2 = 0$, $a_2 = 0$.

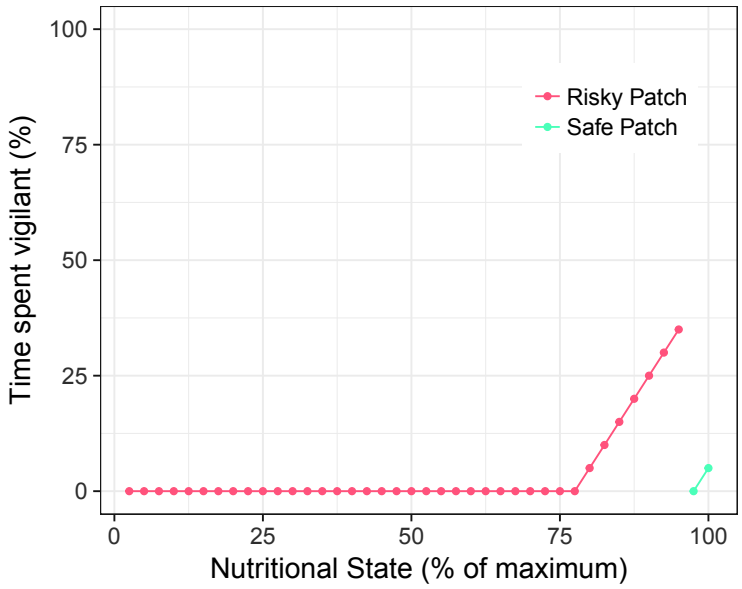


Figure B5 – Optimal choice of vigilance given the nutritional state of a follower in a group of 2 individuals in the risky patch (upper panel) and in the safe patch (lower panel). $f = 0.2$, $k_0(risky) = 0.004$, $k_2 = 0$, $a_2 = 0$.

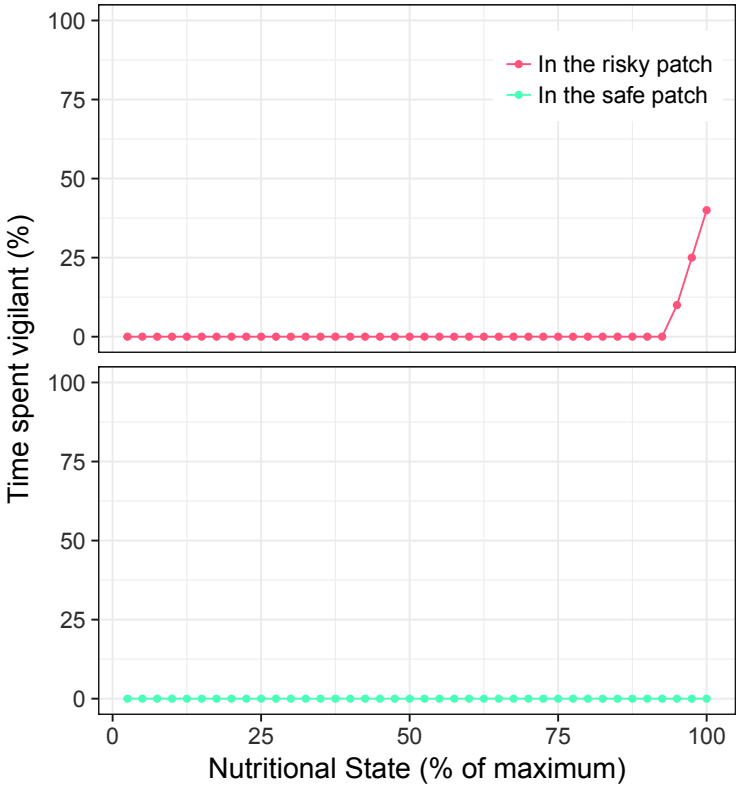
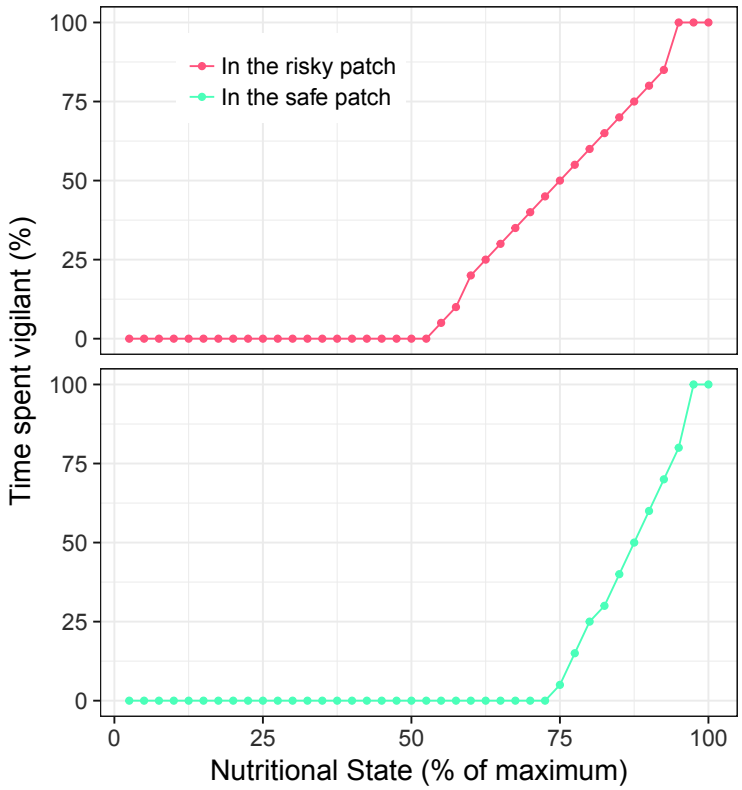


Figure B6 – Optimal choice of vigilance given the nutritional state of a follower with no knowledge of long-term patch use in a group of 2 individuals in the risky patch (upper panel) and in the safe patch (lower panel). $f = 0.2$, $k_0(risky) = 0.004$, $k_2 = 0$, $a_2 = 0$.



Choosing initial nutritional state for simulations

We wanted to initiate an individual nutritional state with the point around which its state will fluctuate, that is to say, its mean nutritional state.. However this cannot be known without any simulations. Based on the optimal strategy only, we can nevertheless approximate such state.

For leaders once we know the optimal strategy, for each nutritional we can calculate the mean food gain provided by this behaviour (vigilance, patch choice). An example is shown in fig. B7. We therefore use as initial state, the state below which behaviour causes an increase in nutritional state (gain larger than cost) and above which behaviour causes a decrease in nutritional state (gain smaller than cost). It is represented by a vertical dashed line on fig. B7.

For followers, we can also calculate the mean gain associated with their behaviour at different nutritional state (fig. B8). We calculated an equilibrium state by simulating a leaders' patch use along with a follower that would always get its mean food gain. The mean nutritional state obtained through this procedure was used to initiate the simulations.

The initial nutritional state that we calculated were used for initiating simulations. Also when a leader died during a follower's simulation, it was immediately replaced by a new leader at its initial state. Overall, the starting states were quite close to the maximum state (as seen by the very high mean nutritional in fig. 3 in the main text).

Figure B7 – Mean food gain given the nutritional state of a leader in a group of 2 individuals. Horizontal dotted line show the mean metabolic cost. Vertical dashed line show the equilibrium state, above which behaviour causes a state decrease and below which it causes a state increase. $f = 0.2$, $k_0(risky) = 0.004$, $k_2 = 0$, $a_2 = 0$.

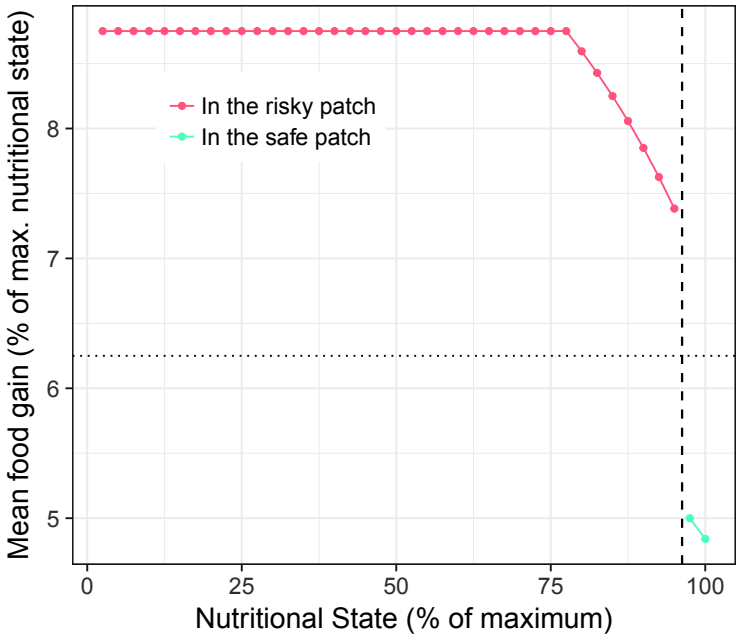
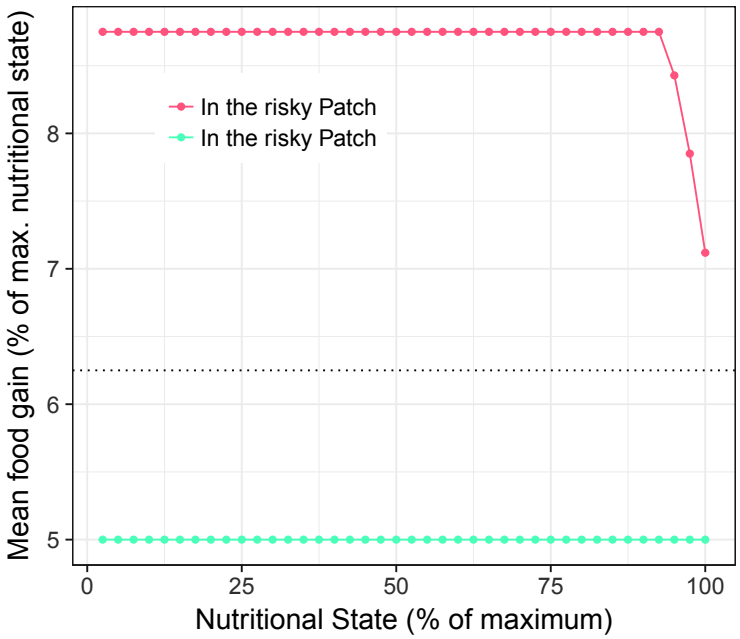


Figure B8 – Mean food gain given the nutritional state and the occupied patch of a follower in a group of 2 individuals. Horizontal dotted line show the mean metabolic cost. $f = 0.2$, $k_0(risky) = 0.004$, $k_2 = 0$, $a_2 = 0$.



Supplement S1. Results from the non-spatial model

This supplementary appendix presents results from the non-spatial model. The only patch available corresponds to the risky and rich patch of the spatial model. By definition there are no followers and leaders, because of the lack of space use decisions. All individuals in a group are therefore similar.

The different figures show the same variables that are presented in the main text (except patch use), that is vigilance (figure S5-1), nutritional state and its variations (figure S5-2), starvation risk, predation risk, and total risk (figure S1-3).

Figure S1-1 – Relationship between time spent vigilant (%, median, lower and upper quartile, in the upper panel) and group size for individuals in groups exploiting only one patch, in situations where the likelihood of meeting the predator is medium (left, $k_1 = 0.004$), high (middle, $k_1 = 0.008$) or very high (right, $k_1 = 0.016$).

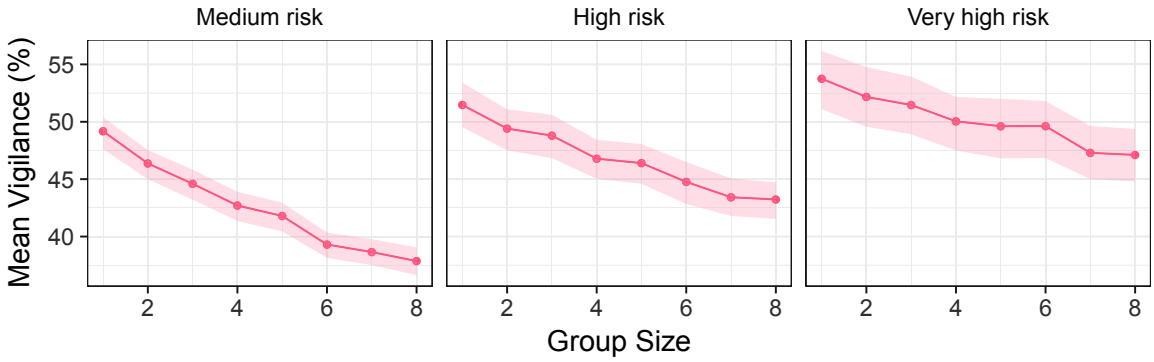


Figure S1-2 – Relationship between mean nutritional state (%, median, lower and upper quartile, in the upper panel) or standard deviation of nutritional state (%, lower panel) and group size for individuals in groups exploiting only one patch, in situations where the likelihood of meeting the predator is medium (left, $k_1 = 0.004$), high (middle, $k_1 = 0.008$) or very high (right, $k_1 = 0.016$).

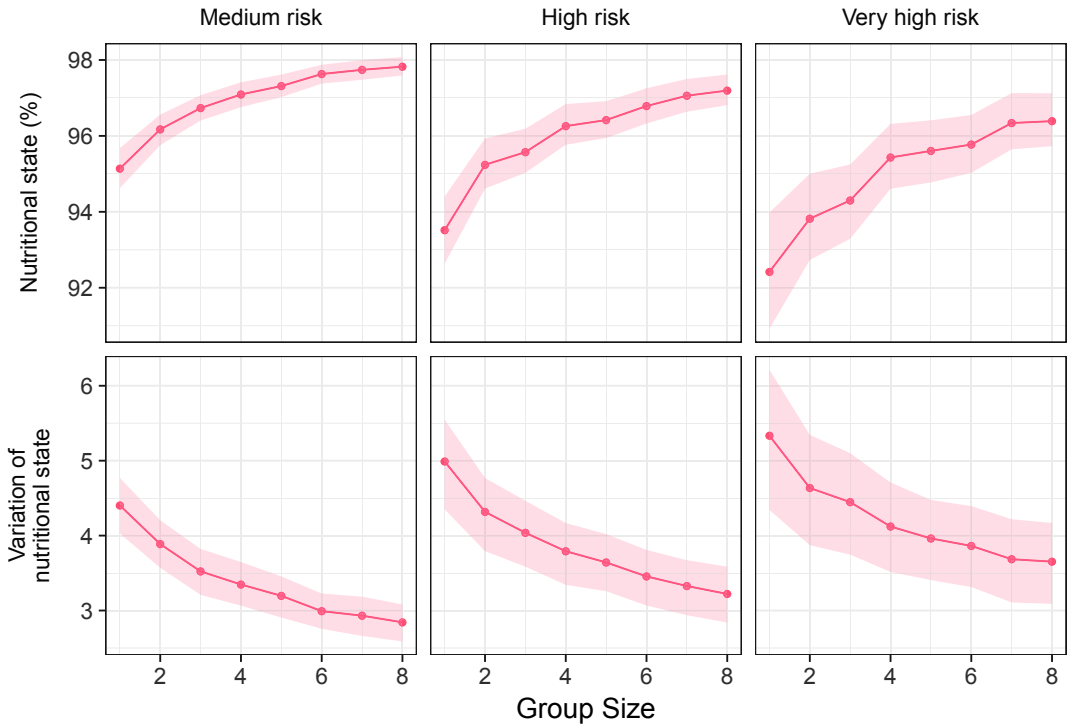
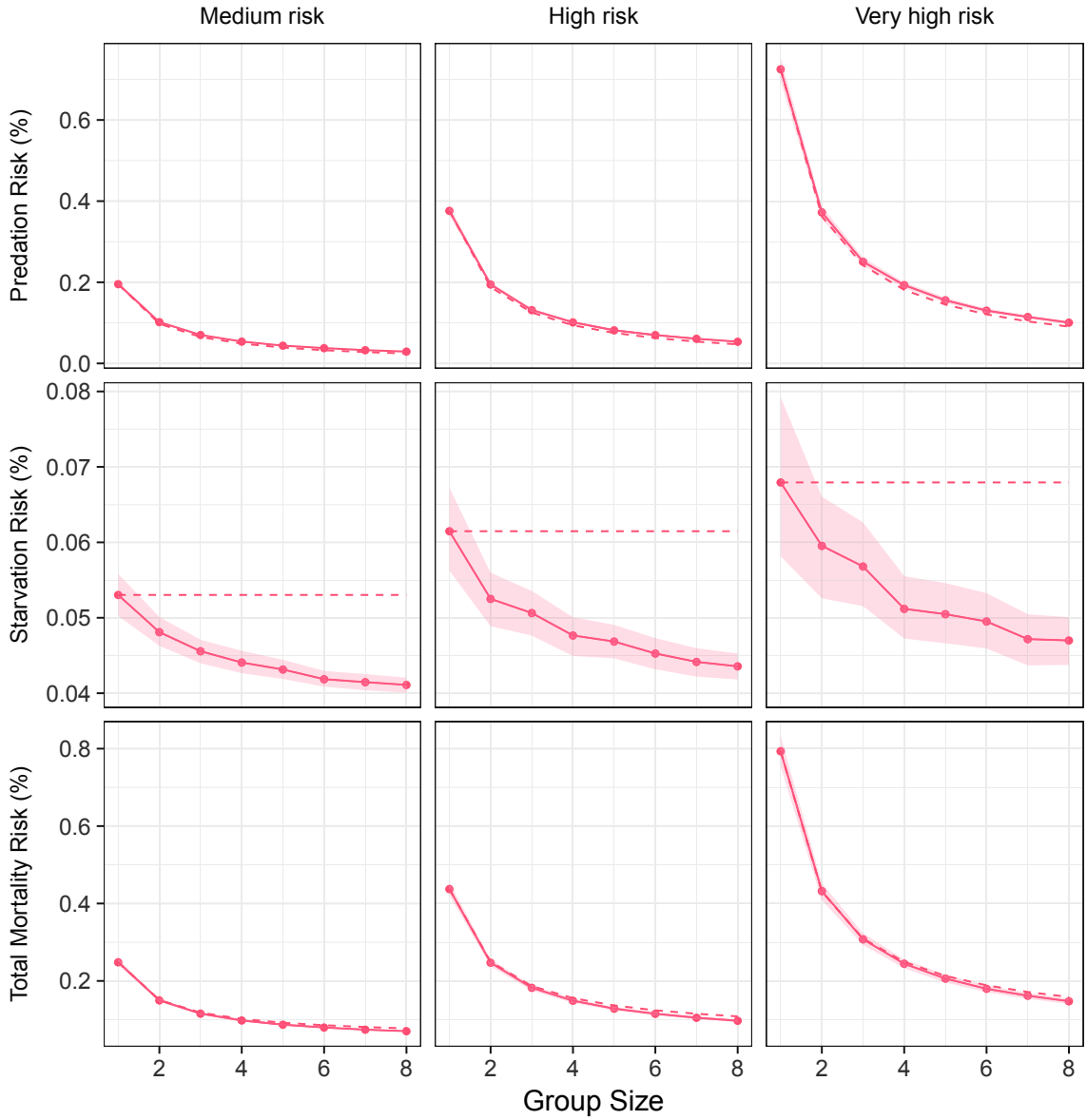


Figure S1-3 – Relationship between mean suffered predation risk (%, median, lower and upper quartile, in the upper panel), mean suffered starvation risk (%, medium panel) or mean suffered total mortality risk (%, lower panel) and group size for individuals in groups exploiting only one patch, in situations where the likelihood of meeting the predator is medium (left, $k_1 = 0.004$), high (middle, $k_1 = 0.008$) or very high (right, $k_1 = 0.016$). Dashed lines show risk for an individual that would adopt the optimal behaviour of a solitary one. Percentages correspond to probabilities of death per simulation time step.



Supplement S2. Additional model outputs

This supplementary appendix shows additional outputs from the model:

1. Figure S2-1 shows mean vigilance accross patches (as shown in main text), mean vigilance in the safe patch and also in the risky patch.
2. Figure S2-2 shows an example of 60 steps of model run for a follower and a leader, under condition of medium risk in risky patch.

Patch-specific vigilance

We can see on figure S2-1:

- that mean vigilance in the safe patch is either null or very low (lower panel).
- that relative differences of mean vigilance accross patches (upper panel) follow the same pattern as relative differences of mean vigilance in the risky patch (middle panel).

Example of model run

Figure S2-2 shows a model run during 60 time steps. Groups alternate between the risky and the safe patch depending on the leader nutritional state. In this example, when the leader nutritional state is equal or lower to 95%, the leader switches to the risky patch. At some point, if the leader can maintain its state voer 95% for a long time while in the safe patch (e.g. between time step 294 and 300). In the meantime, a luckless follower can see its state drops from nearly 95% to 80%, and its associated starvation risk rise. In other instance in the safe patch (time steps 275 to 278) a follower can maintain its nutritional state at nearly 100% while the one of the leader drops and force him to go with the group to the risky patch.

The optimal strategy of a follower forces him to minimize the risk of a run of bad luck (as seen between time steps 294 and 300) that would increase highly its mortality risk. For that reason, a follower will be less vigilant than a leader to anticipate that it might not be in the risky patch when its states drops.

Note that the follower is sometimes more vigilant than the leader. Indeed when a follower is at maximum state in the risky patch, there is no need to be foraging at maximum capacity, because states cannot go higher. In opposition, a leader at maximum state would choose to go in the safe patch and be nearly non-vigilant.

Figure S2-1 – Relationship between mean time spent vigilant (%, median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch. Time spent vigilant is shown accross patches (upper panel), in the risky patch (middle panel) and in the safe patch (lower panel)

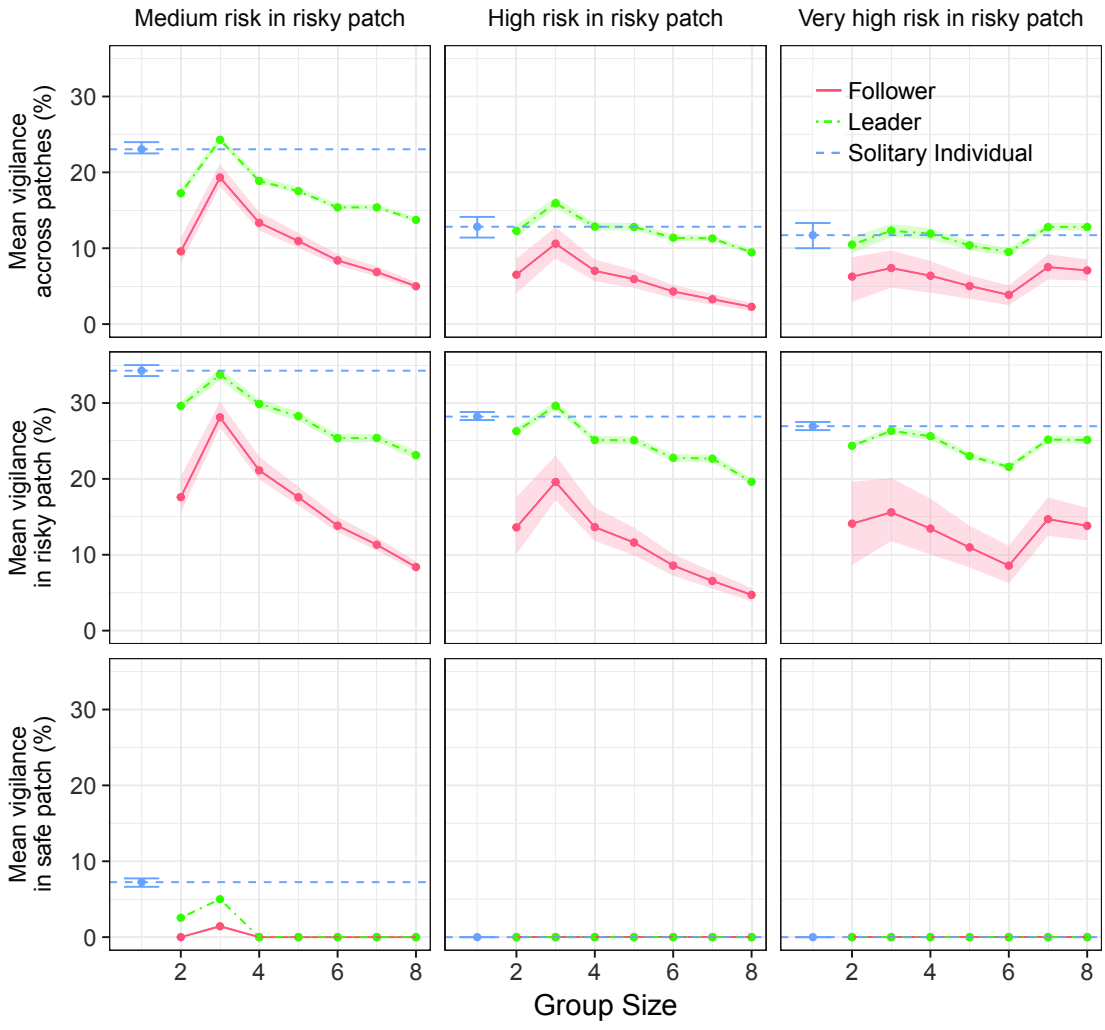
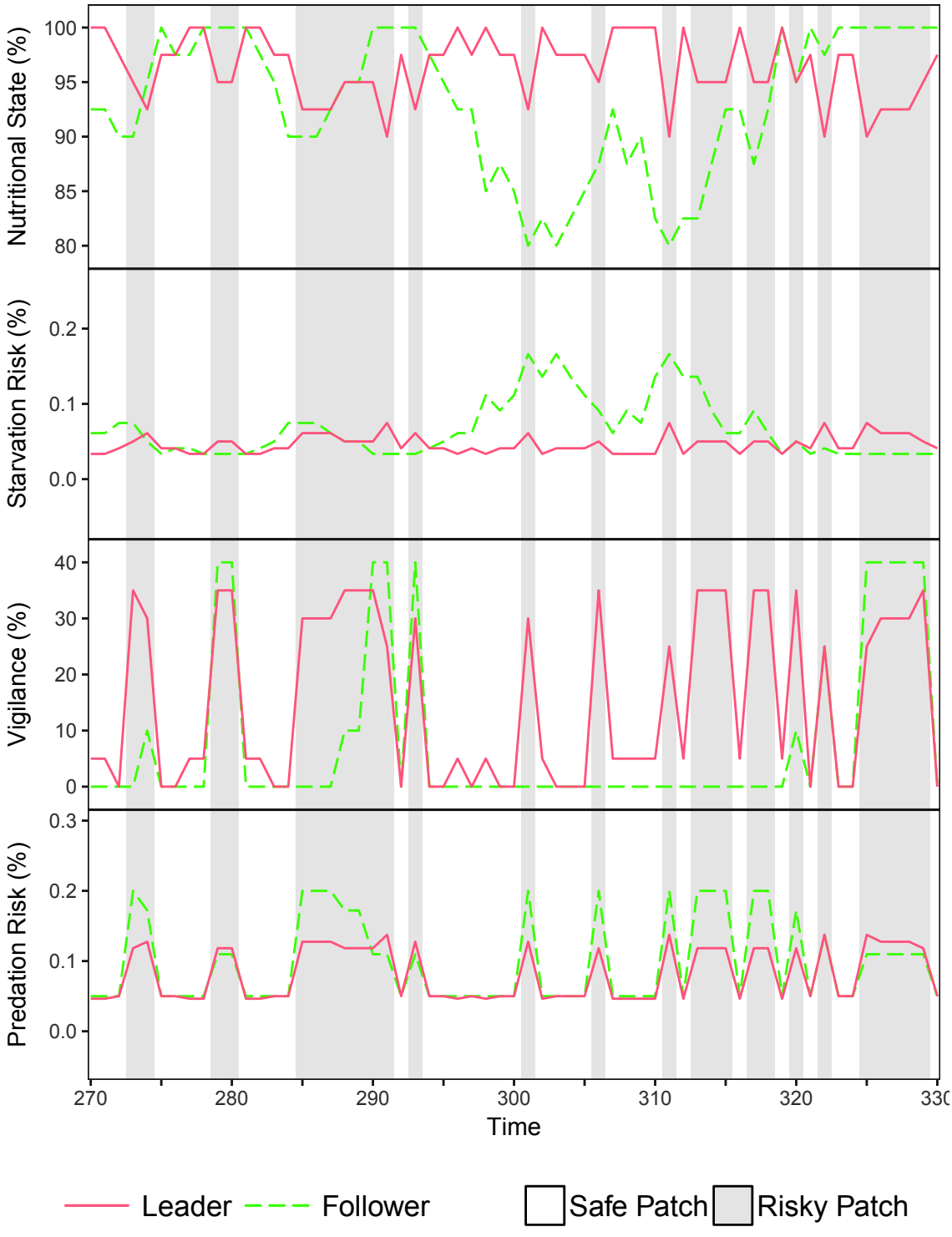


Figure S2-2 – Example of a model run for 60 steps. Red lines shows leader behaviour while green dashed lines shows follower behaviour. Use of risky patch is shown by grey-shaded areas. Simulations were run considering a medium risk in the risky patch and a group of two individuals. Percentages for predation and starvation risk correspond to probabilities of death per simulation time step.



Supplement S3. Results for different strength of starvation risk

This supplementary appendix presents results for different parameters of starvation risk strength (f, see equation 3). In the main article we showed results only for a high starvation risk ($f = 0.2$), but here we added results for medium and low starvation risk ($f = 0.25$ and $f = 0.3$). Under higher values of f, starvation risk was too low, and no dilution effect was observed (there were not enough benefits for increasing foraging).

The different figures show the same variables that are presented in the main text, that is vigilance (figure S5-1), patch use (figure S4-4), nutritional state and its variations (figure S5-2 and S4-6), starvation risk (figure S5-3), predation risk (figure S4-8) and total risk (figure S4-9).

See the main text for the presentation and discussion of these results.

Figure S3-1 – Relationship between mean time spent vigilant accross patches (%, median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel).

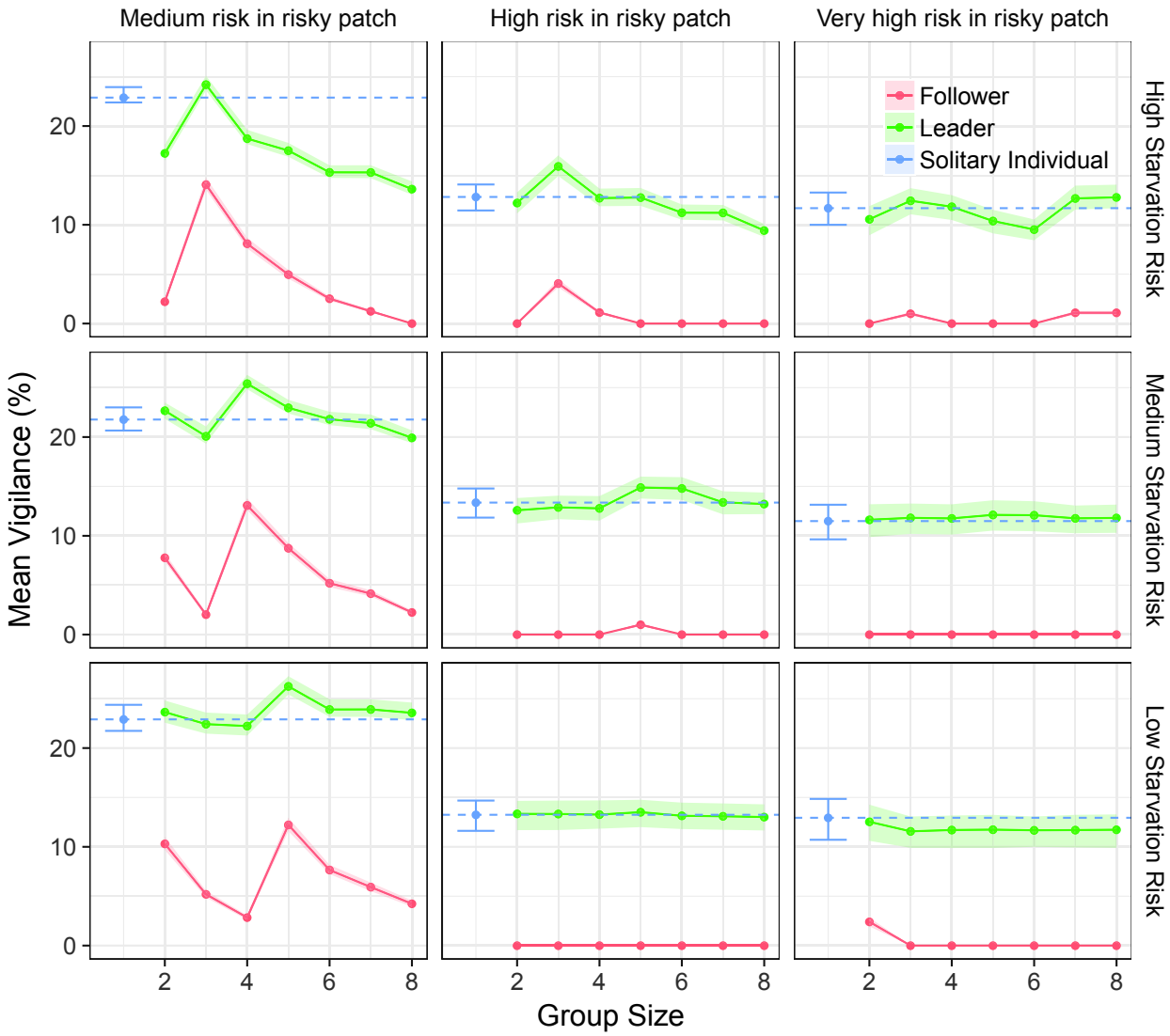


Figure S3-2 – Relationship between time spent in the risky patch (%, median, lower and upper quartile) and group size for solitary individuals (blue) and group leaders (green), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel). Follower patch use is not shown because it is identical to the one of the leader.

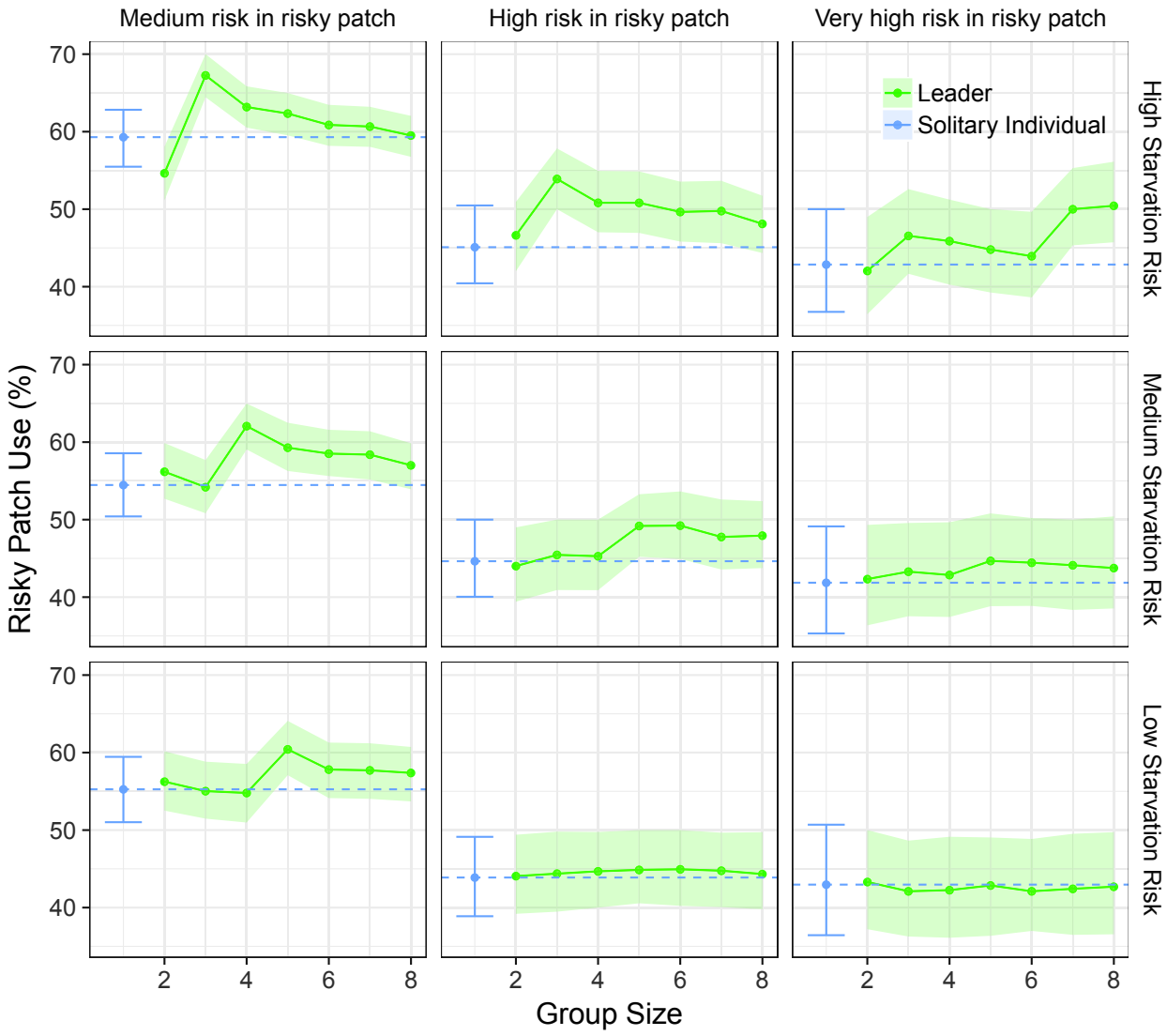


Figure S3-3 – Relationship between mean nutritional state (%, median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel).

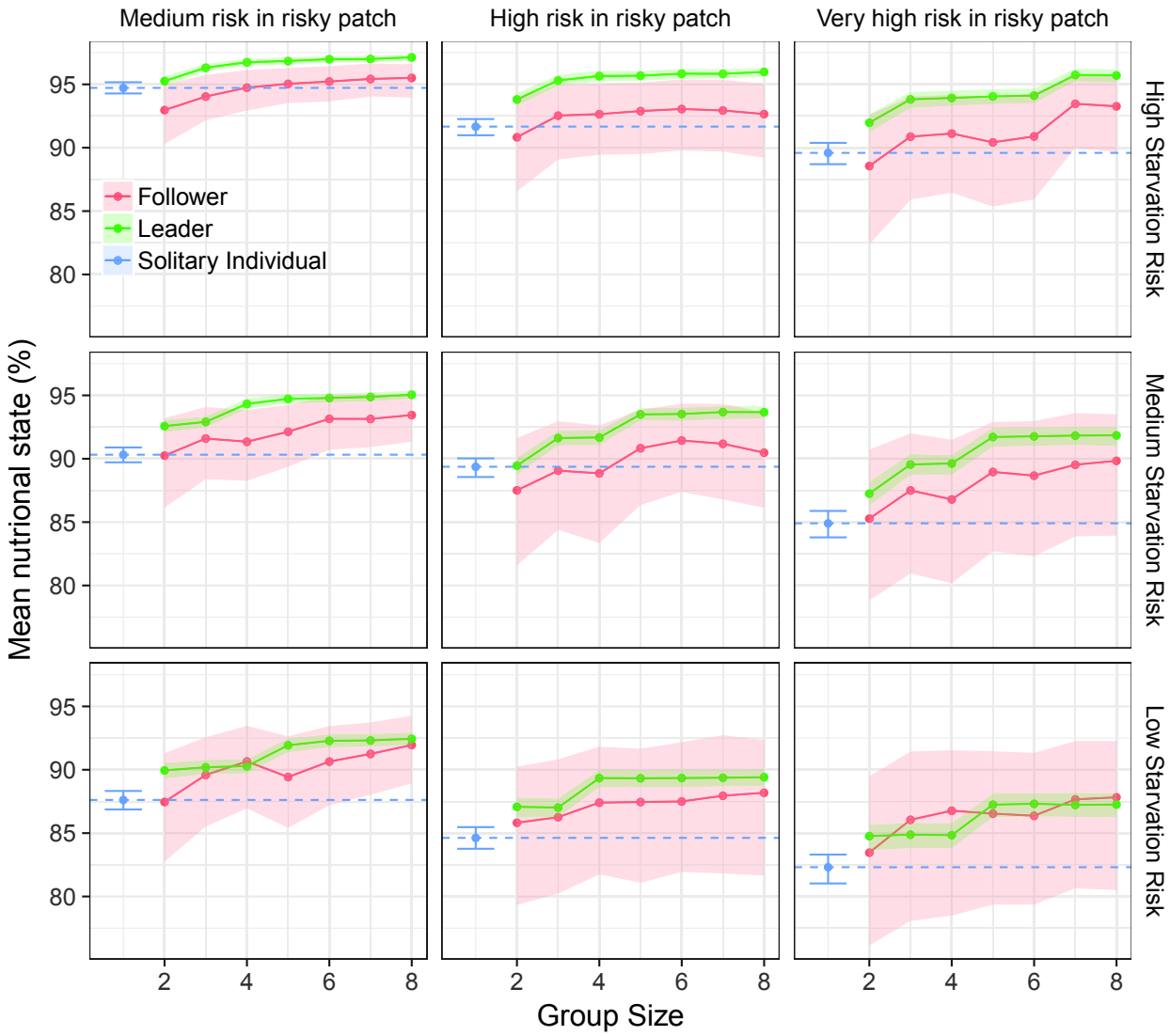


Figure S3-4 – Relationship between standard deviation of nutritional state (%, median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel).

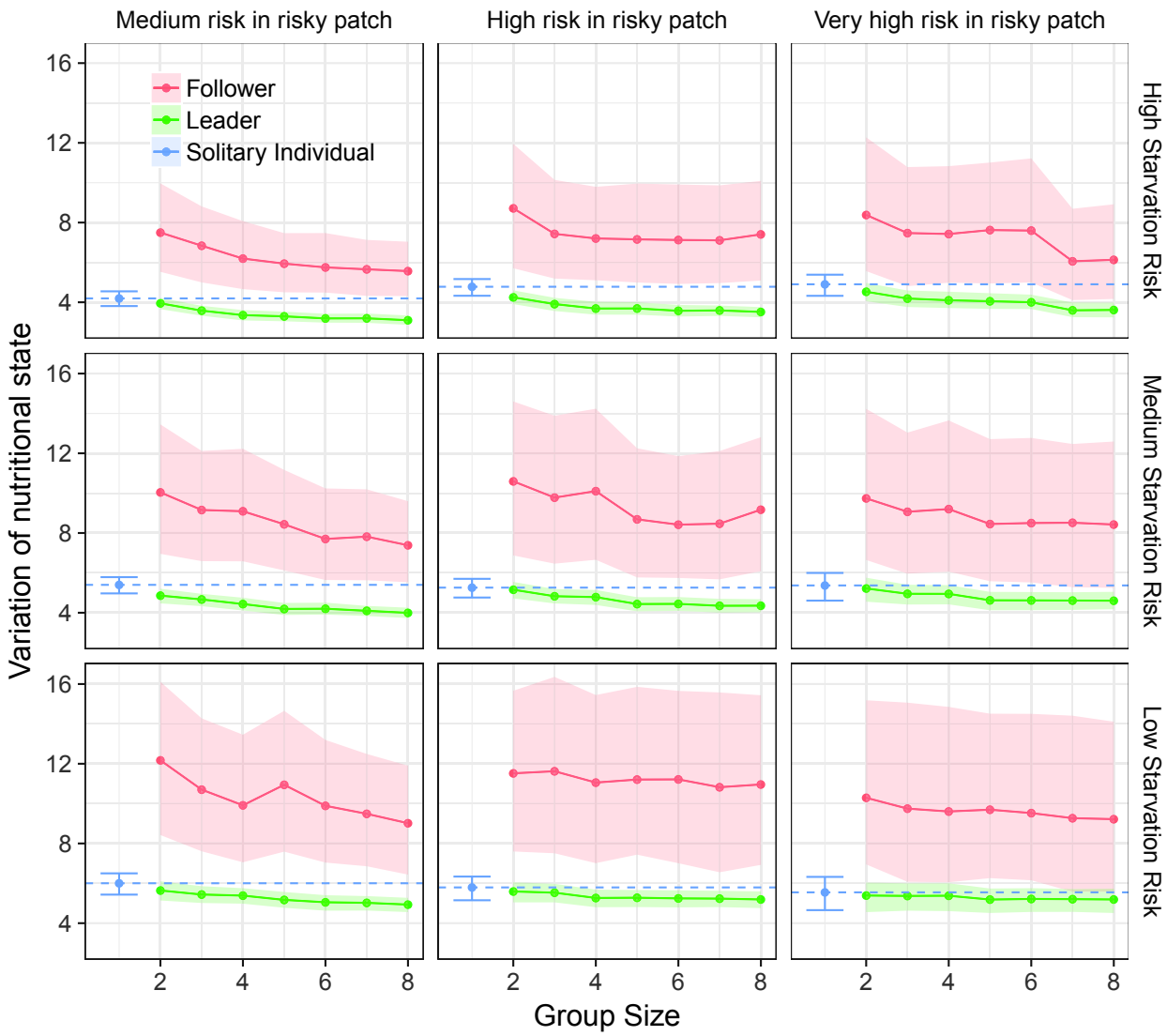


Figure S3-5 – Relationship between mean suffered starvation risk (%, median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel). Percentages correspond to probabilities of death per simulation time step.

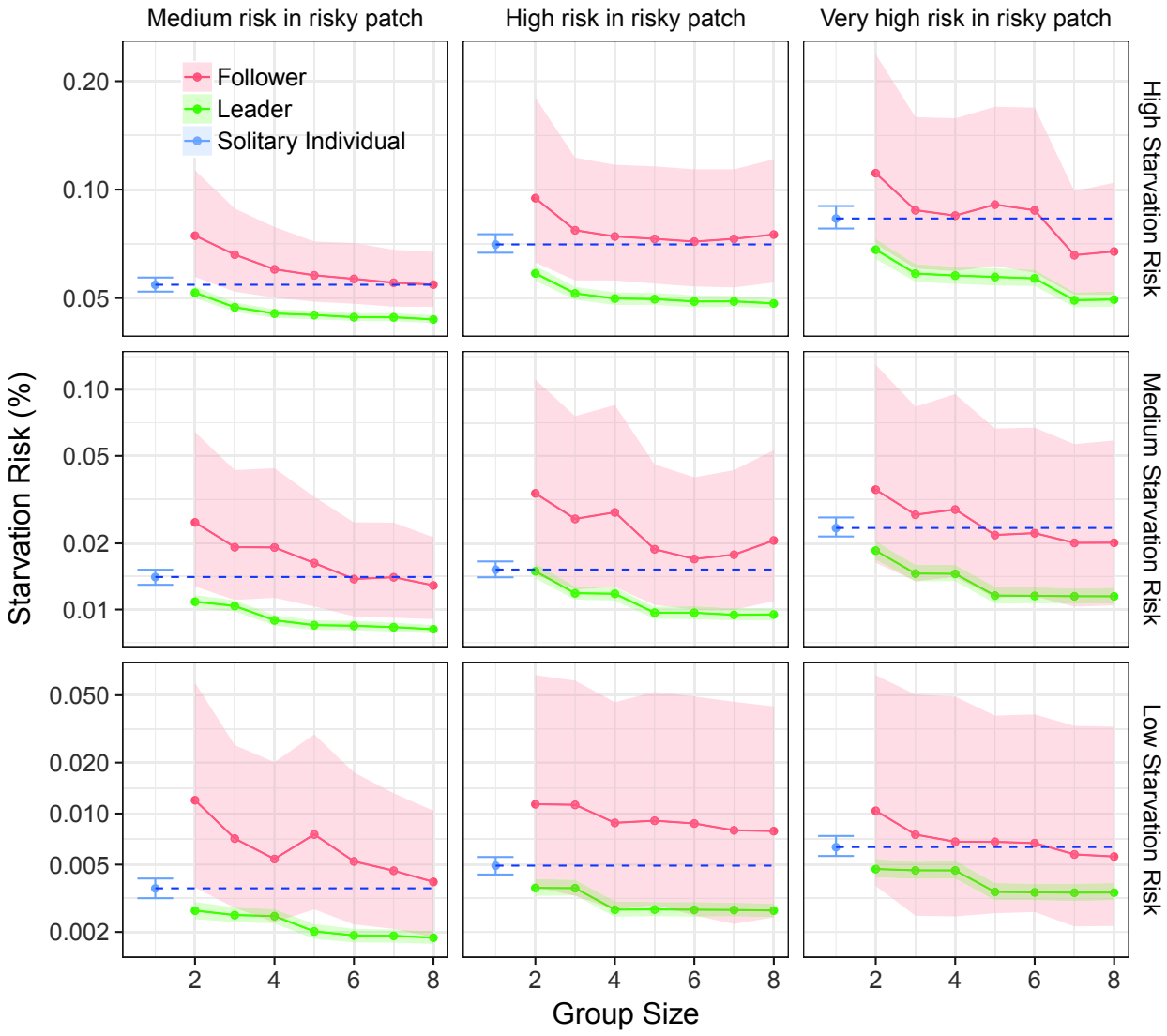


Figure S3-6 – Relationship between mean suffered predation risk (%, median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel). Dashed lines show predation risk of a leader that would adopt the optimal behaviour of a solitary individual. Percentages correspond to probabilities of death per simulation time step.

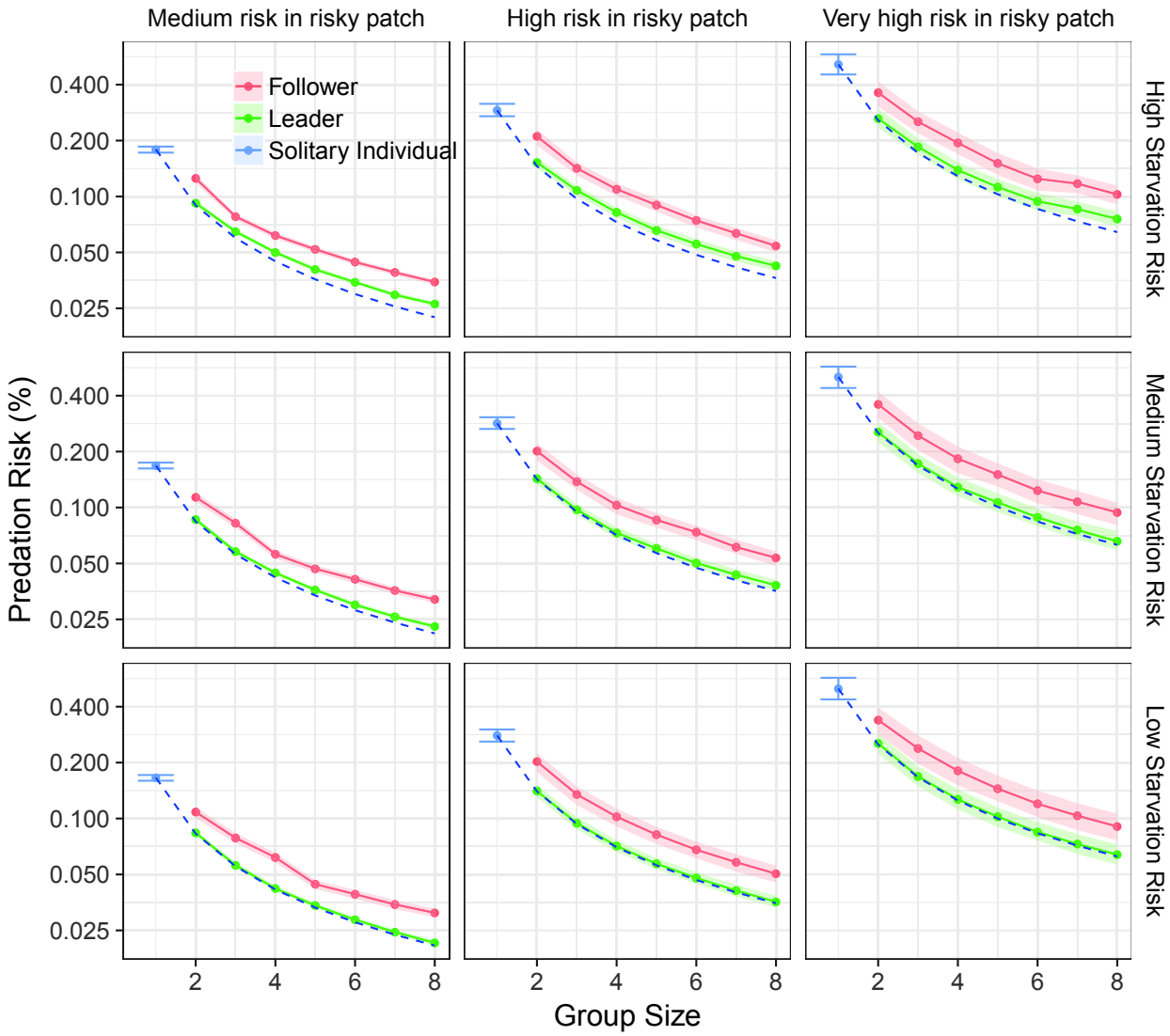
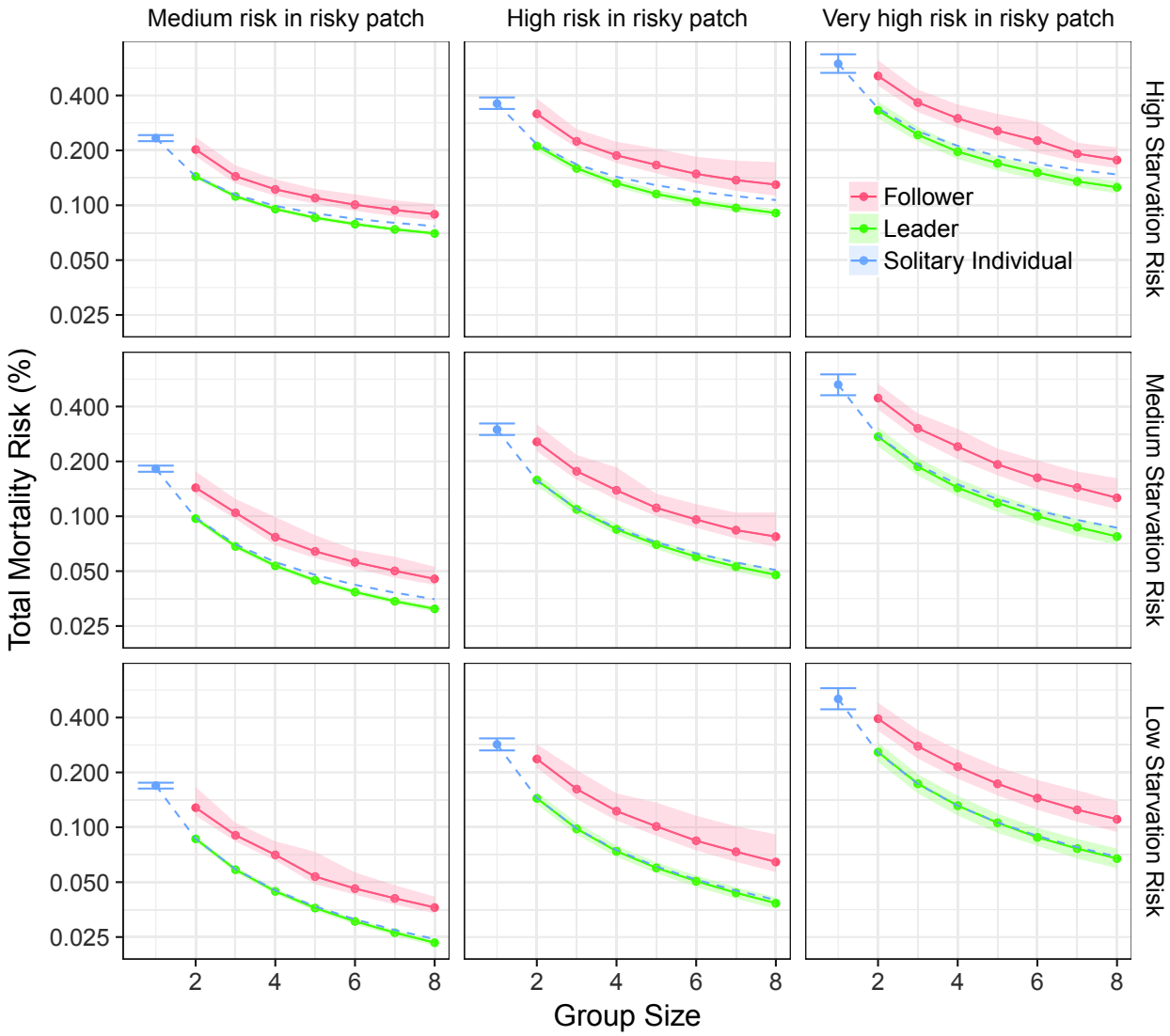


Figure S3-7 – Relationship between mean suffered mortality risk (%, median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel). Dashed lines show mortality risk of a leader that would adopt the optimal behaviour of a solitary individual. Percentages correspond to probabilities of death per simulation time step.



Supplement S4. Results under alternative assumptions about encounter rates with predators and with food items

This supplementary appendix presents results obtained under different assumptions about (i) the link between predator encounter rate and group size and (ii) the link between encounter rate with food items and vigilance.

Assuming that predator encounter rate increases with group size

Increasing group size also incurs additional costs that we did not account for, such as coordination effort (see e.g. Sueur (2012)) or increased detectability by predator (Hebblewhite and Pletscher 2002). In particular, we assumed that group size did not change the likelihood that the group meets the predator and that one individual is attacked. Although we studied the increase in group by only a few individuals, the validity of this assumption can be questioned. Previous modelling studies have sometimes relaxed this assumption (Turner and Pitcher 1986), and empirical data suggests that indeed sometimes larger groups are more easily detected and targeted by predators (Krause and Godin 1995), although not always (Quinn and Cresswell 2004). Higher detectability of larger groups could lead to increased vigilance and increased use of safer patches in larger groups, compared to our results. As discussed in the main text, the specific changes in behavior (whether vigilance or space-use will change to a riskier behavior with increasing group size) are likely to be sensitive to exactly how group size affects encounter rate. Therefore, relaxing this assumption will certainly change the shape of the vigilance – group size relationship in a context-specific way. The change in assumption, however, should not affect the differences of behaviour between leaders and followers.

In this appendix, we forced the predator encounter rate to increase with group size, following the equation below, which is modified from equation (2) in the main text.

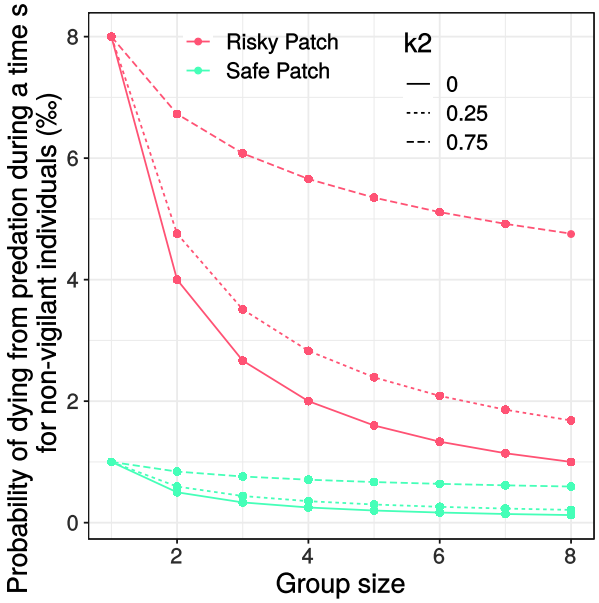
$$Pred(t) = k_0(p(t)) \times \mathrm{N}^{k_2} \times \frac{1}{\mathrm{N}} \times e^{-k_1 v(t)} \tag{B12}$$

Basal encounter rate k_0 is now multiplied by N^{k_2}. If $k_2 = 0$ there is no increase of encounter rate, but if $k_2 > 0$, encounter rate increases with group-size. The higher k_2, the lower are the benefits of risk dilution. Figure S4-1 shows how an increase of predator encounter risk with group size change the predation risk for a non-vigilant individual.

Assuming a non-linear decrease of food items encounter rate with vigilance

Instead of assuming that encounter rate with food items was linearly related to vigilance (see equation 1 in main text) we tested different non-linear relationship between

Figure S4-1 – Relationship between probability of dying from predation and group size for a non vigilant individual in the safe and pour patch (blue) or the risky and rich patch (red), under different assumptions about the increase of predator encounter rate with group size : no increase of encounter rate with group size (plain line), large increase (dashed line), very large increase (double dashed line).



encounter rate and vigilance, with encounter rate decreasing either slower or faster than with a linear relationship. We assumed that:

$$a = a_0 \times (1 - v^{1+a_1}) \tag{B13}$$

with a the encounter rate with food items, a_0 maximum encounter rate, v vigilance and a_1 the parameter controlling the non linearity of the relationship. If $a_1 = 0$ the relationship is linear. If $a_1 < 0$ encounter rate decreases faster than expected under linear assumptions. This makes vigilance more costly because an increase would decrease foraging more than expected under a linear assumption.

Also, if $a_1 > 0$ encounter rate decreases slower than expected under linear assumption. This makes vigilance more efficient because an increase would would decrease foraging less than expected under a linear assumption.

The functional relationship between vigilance and food gain is shown on figure S4-2 for the different values of a_1.

Results

The different figures show the same variables presented in the main text, that is vigilance (figure S5-1), patch use (figure S4-4), nutritional state and its variations (figure S5-2 and S4-6), starvation risk (figure S5-3), predation risk (figure S4-8) and total mortality risk (figure S4-9).

See the main text for a presentation and discussion of the results.

Figure S4-2 – Relationship between food gain and vigilance for the safe and pour patch (blue) and the risky and rich patch (red), in situations where encounter rate with food items decrease either faster than linear (plain line, same as main text results), linearly (dashed line) or faster than linear (double dashed line).

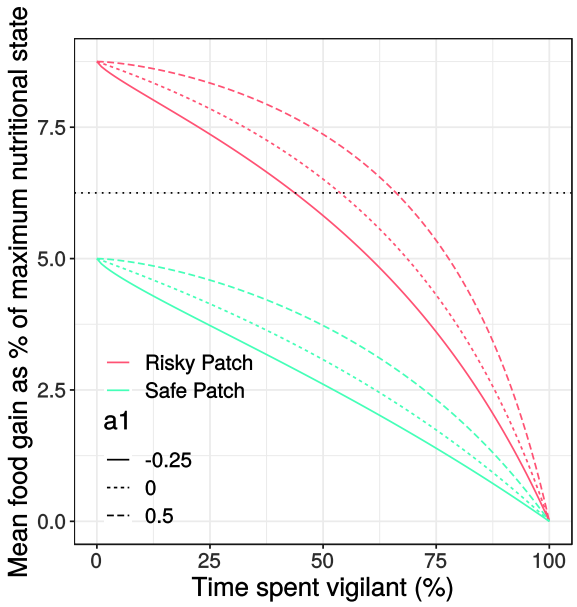


Figure S4-3 – Relationship between mean time spent vigilant accross patches (%, median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator does not change ($k_2 = 0$, left), increases slightly ($k_2 = 0.25$, middle) or largely ($k_2 = 0.75$, right) with group size and attack rate deacreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance.

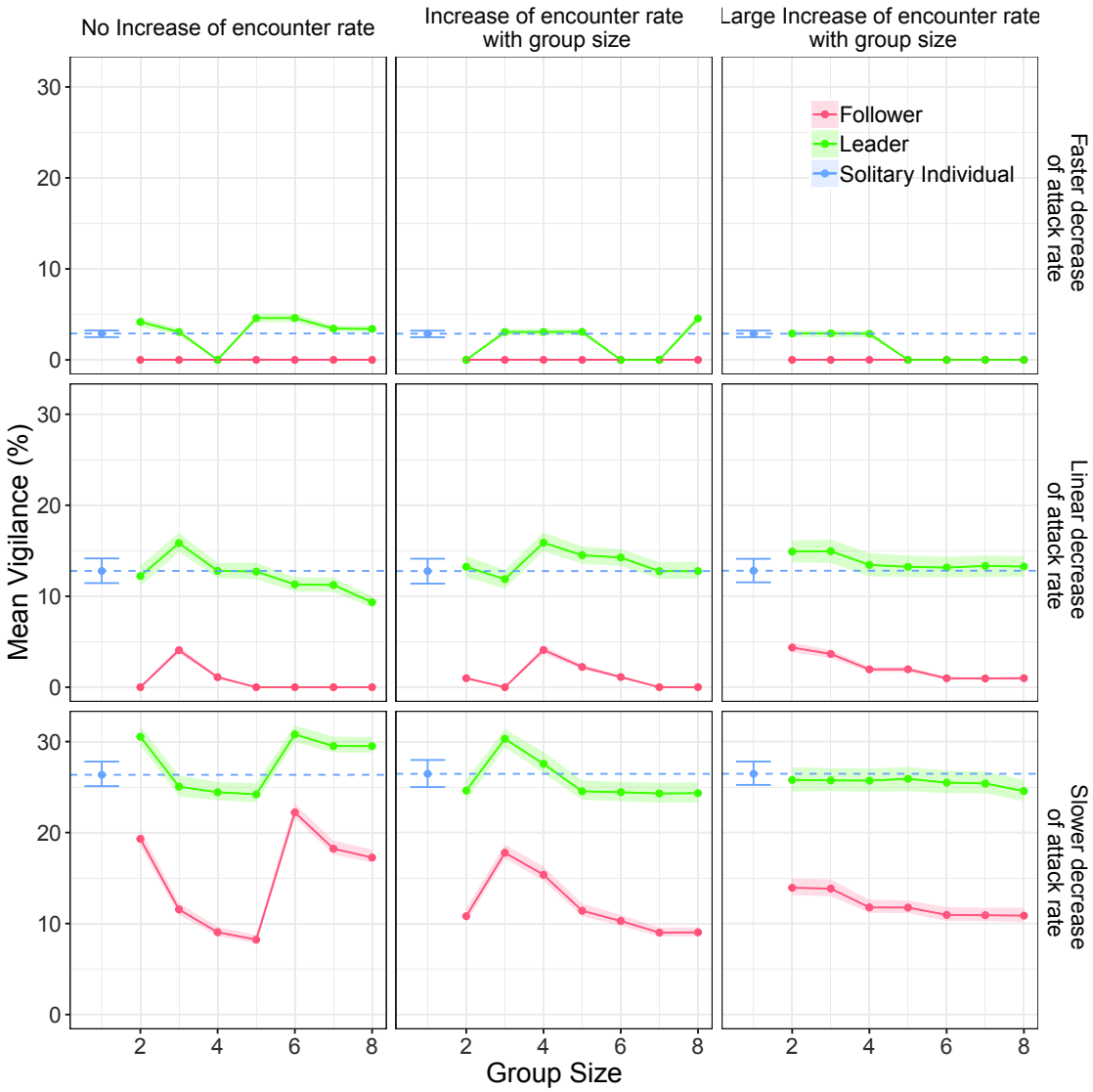


Figure S4-4 – Relationship between time spent in the risky patch (%, median, lower and upper quartile) and group size for solitary individuals (blue) and group leaders (green), in situations where the likelihood of meeting the predator does not change (k_2 = 0, left), increases slightly (k_2 = 0.25, middle) or largely (k_2 = 0.75, right) with group size and attack rate deacreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance. Follower patch use is not shown because it is identical to the one of the leader.

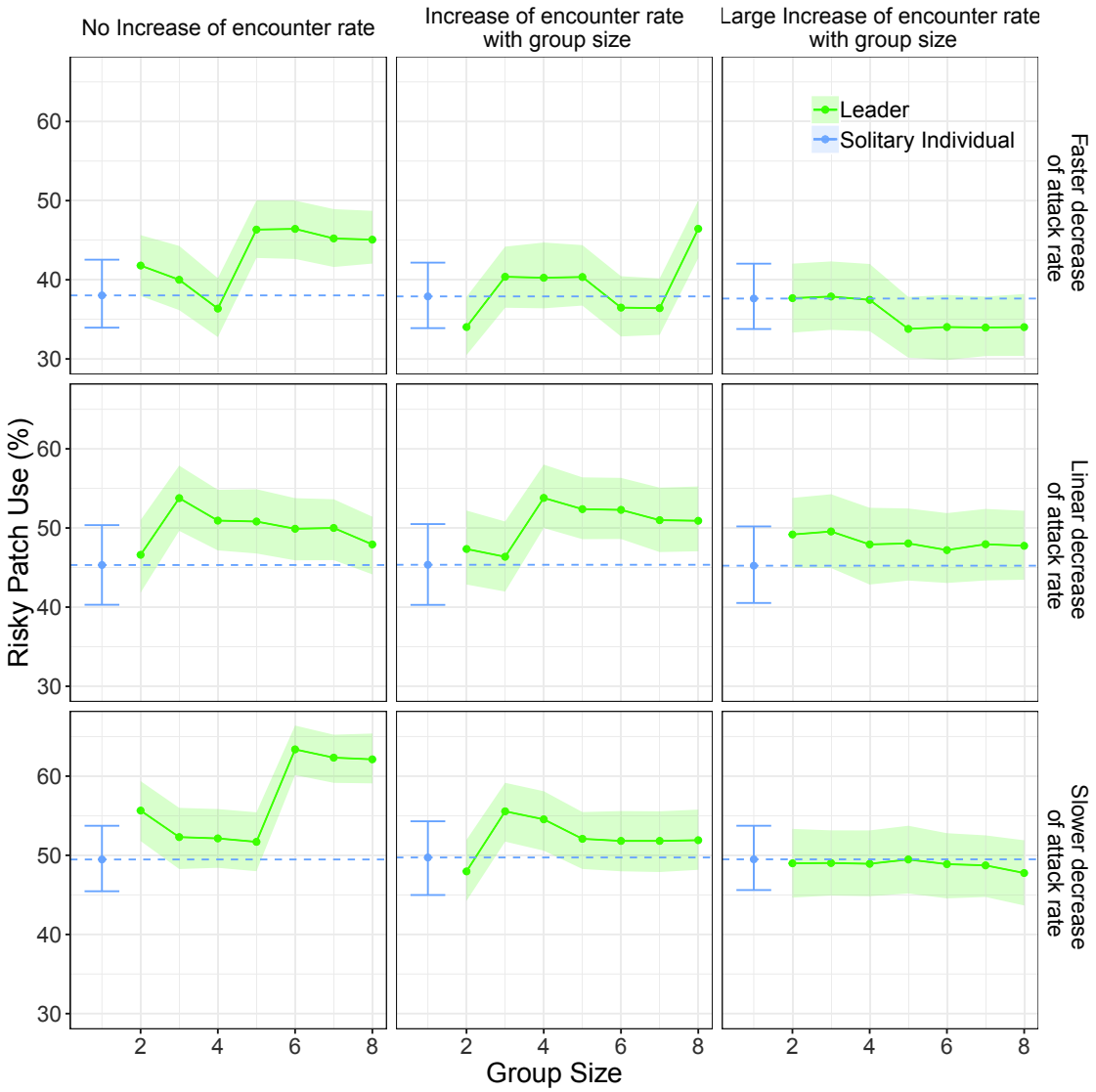


Figure S4-5 – Relationship between mean nutritional state (%, median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator does not change ($k_2 = 0$, left), increases slightly ($k_2 = 0.25$, middle) or largely ($k_2 = 0.75$, right) with group size and attack rate deacreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance.

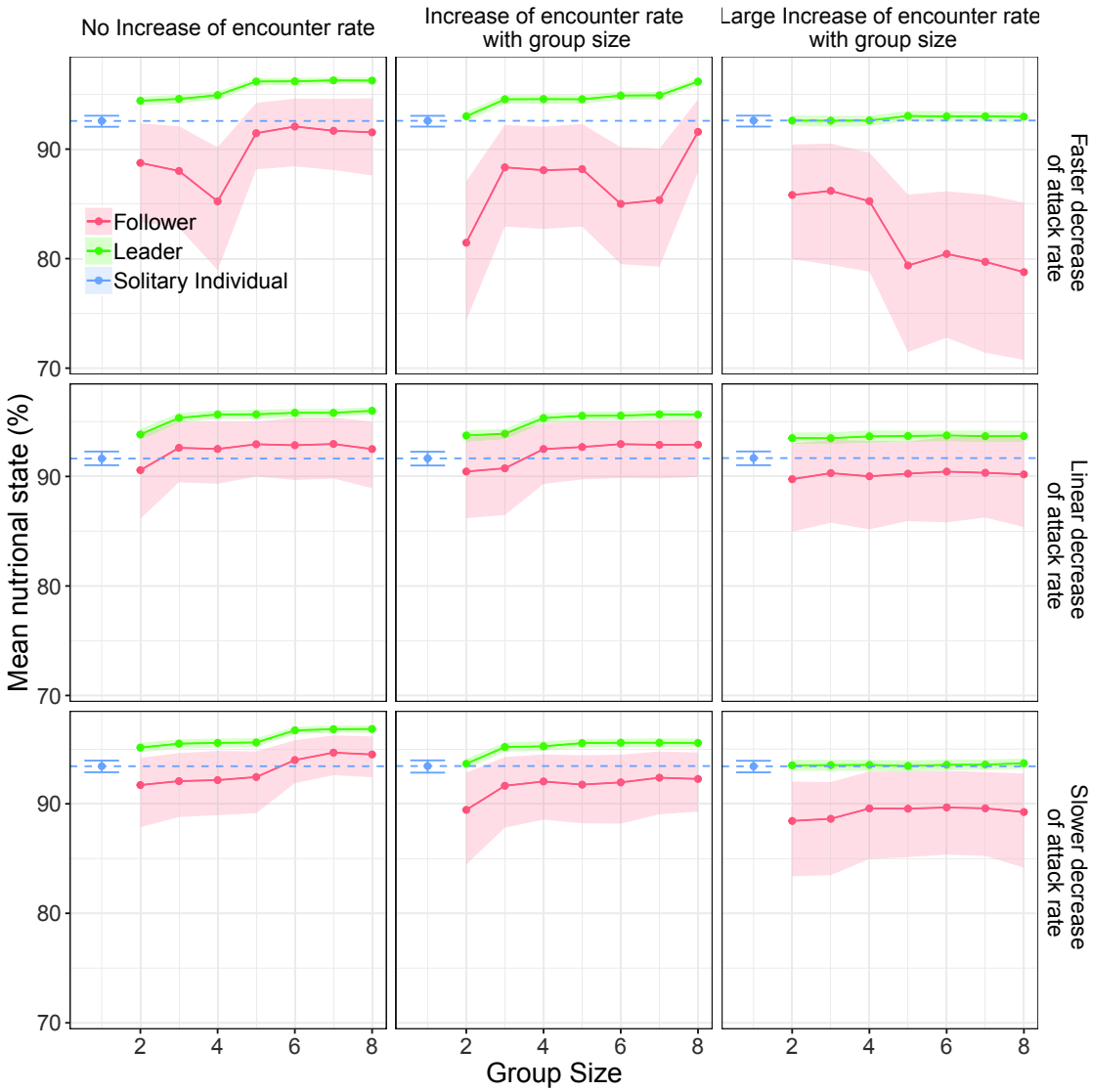


Figure S4-6 – Relationship between standard deviation of nutritional state (%, median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator does not change ($k_2 = 0$, left), increases slightly ($k_2 = 0.25$, middle) or largely ($k_2 = 0.75$, right) with group size and attack rate deacreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance.

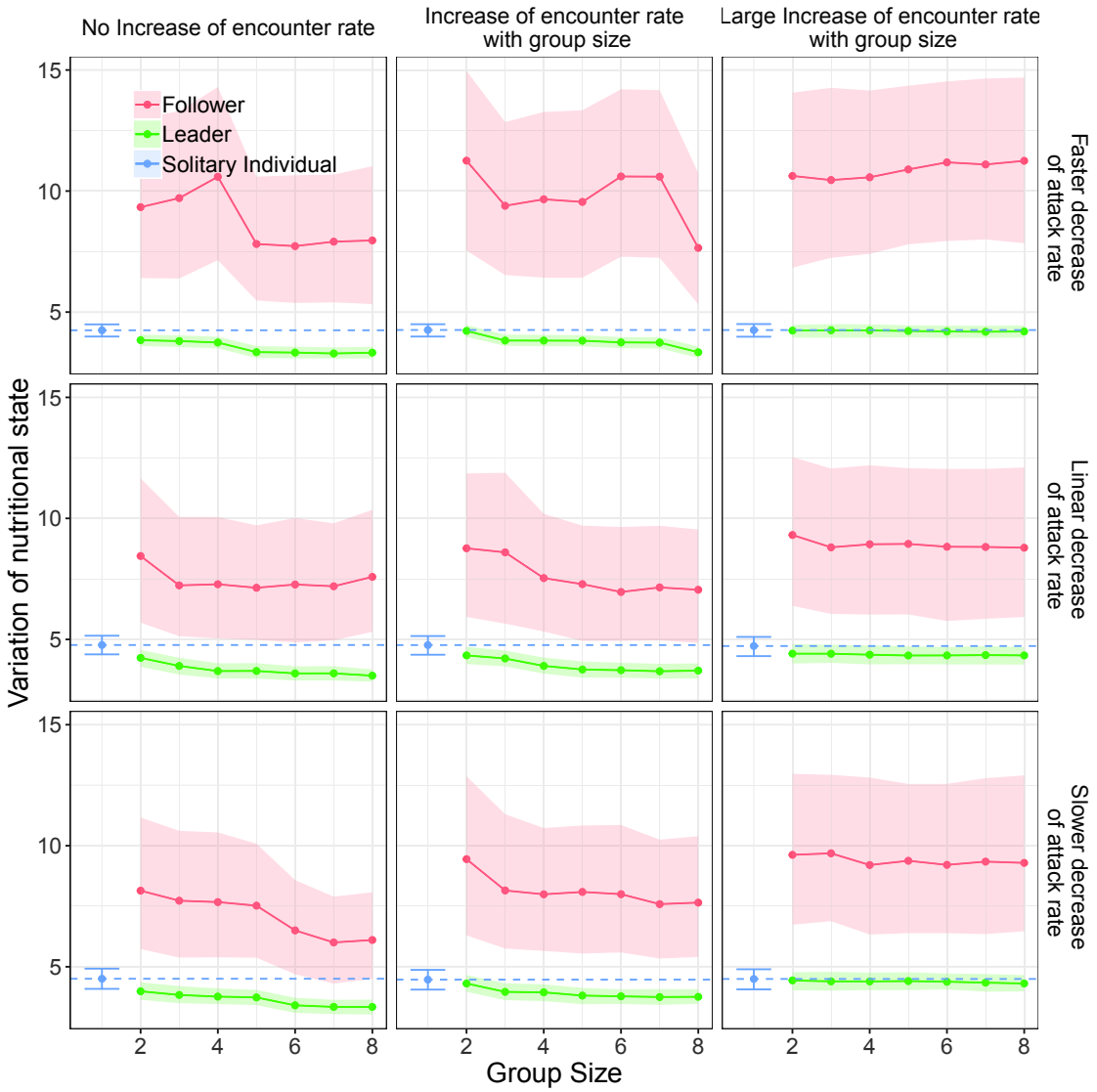


Figure S4-7 – Relationship between mean suffered starvation risk (%, median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator does not change ($k_2 = 0$, left), increases slightly ($k_2 = 0.25$, middle) or largely ($k_2 = 0.75$, right) with group size and attack rate deacreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance. Percentages correspond to probabilities of death per simulation time step.

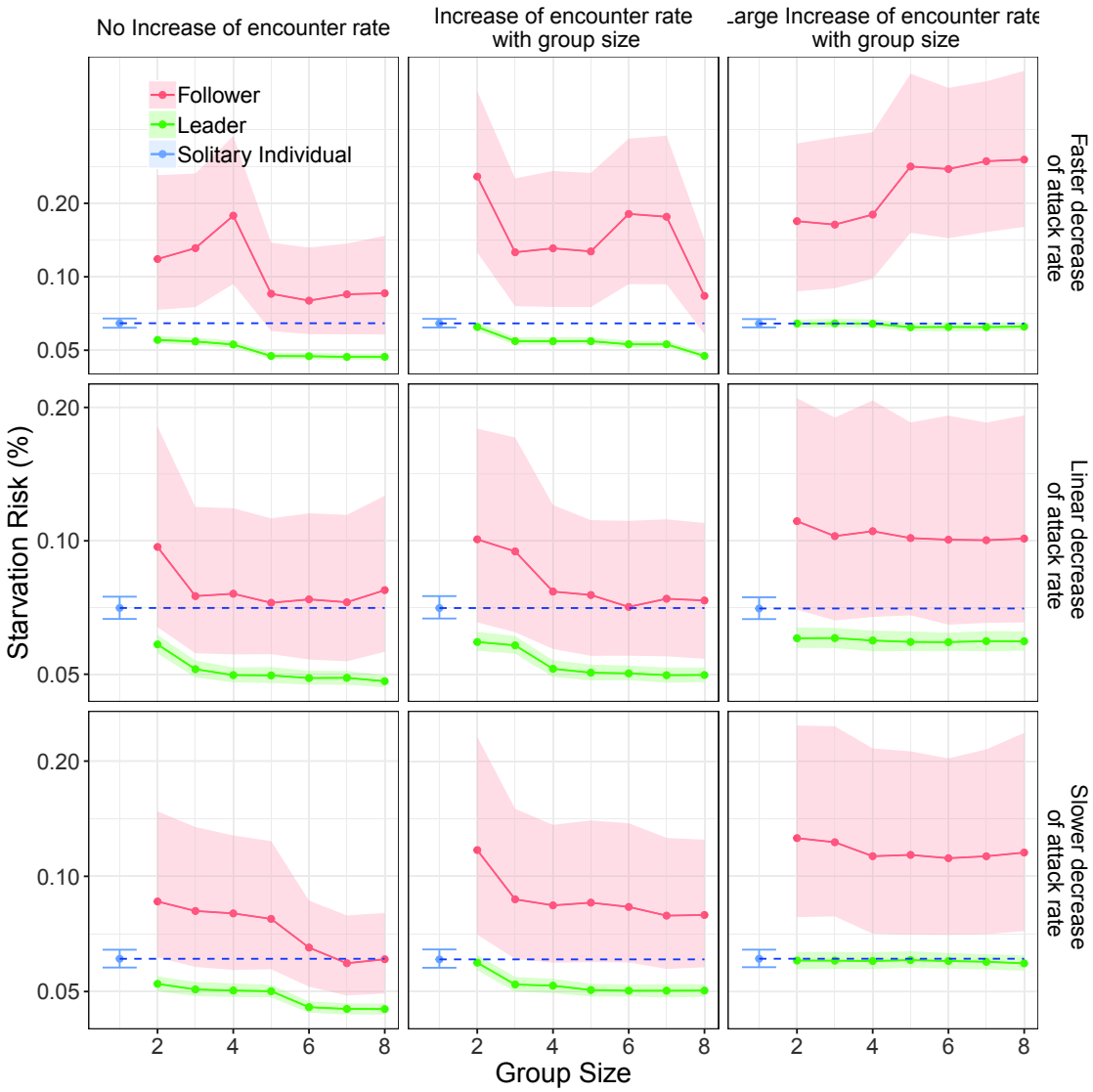


Figure S4-8 – Relationship between mean suffered predation risk (%, median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator does not change ($k_2 = 0$, left), increases slightly ($k_2 = 0.25$, middle) or largely ($k_2 = 0.75$, right) with group size and attack rate deacreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance. Dashed lines show predation risk of a leader that would adopt behaviour of a solitary individual. Percentages correspond to probabilities of death per simulation time step.

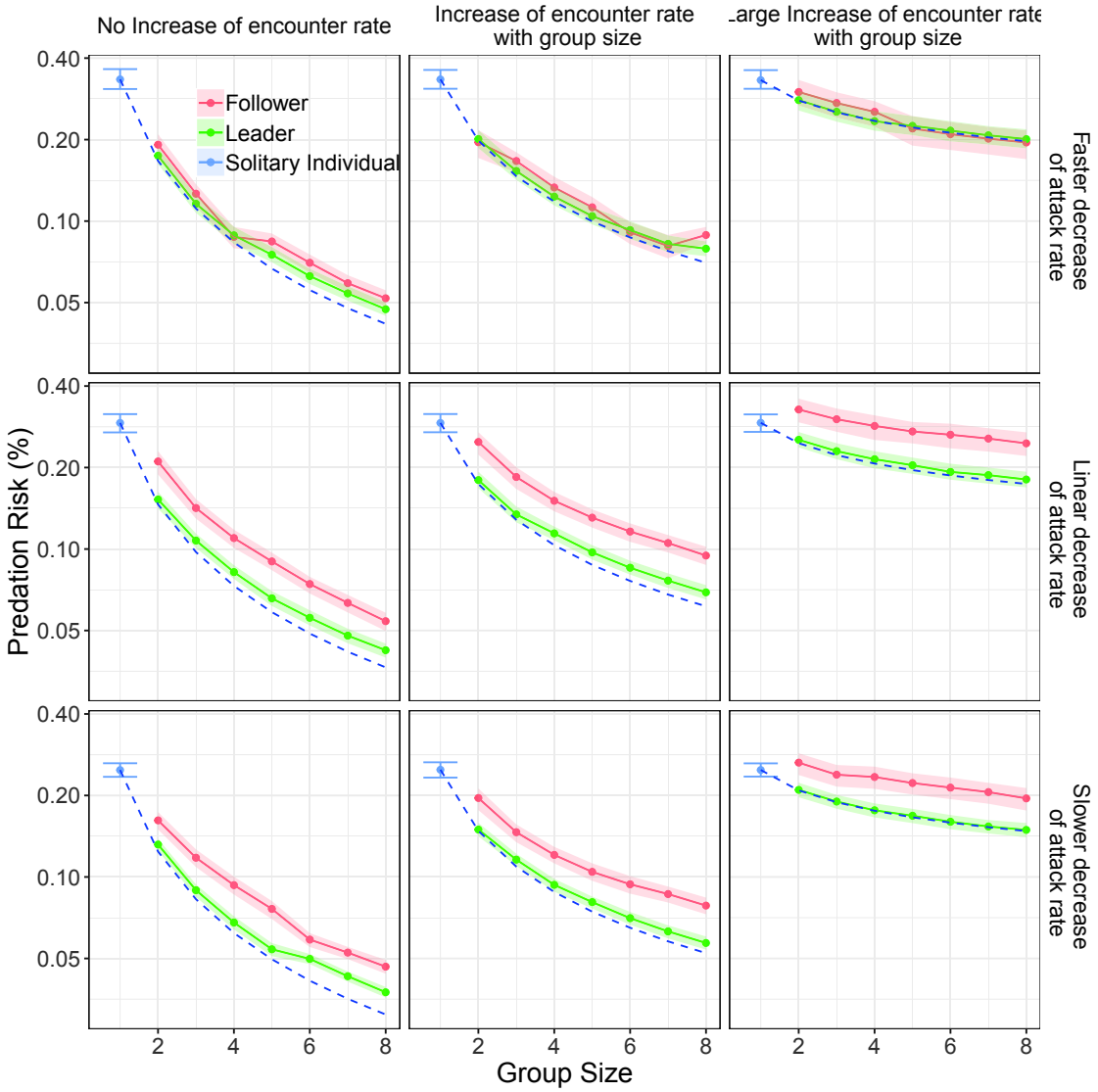
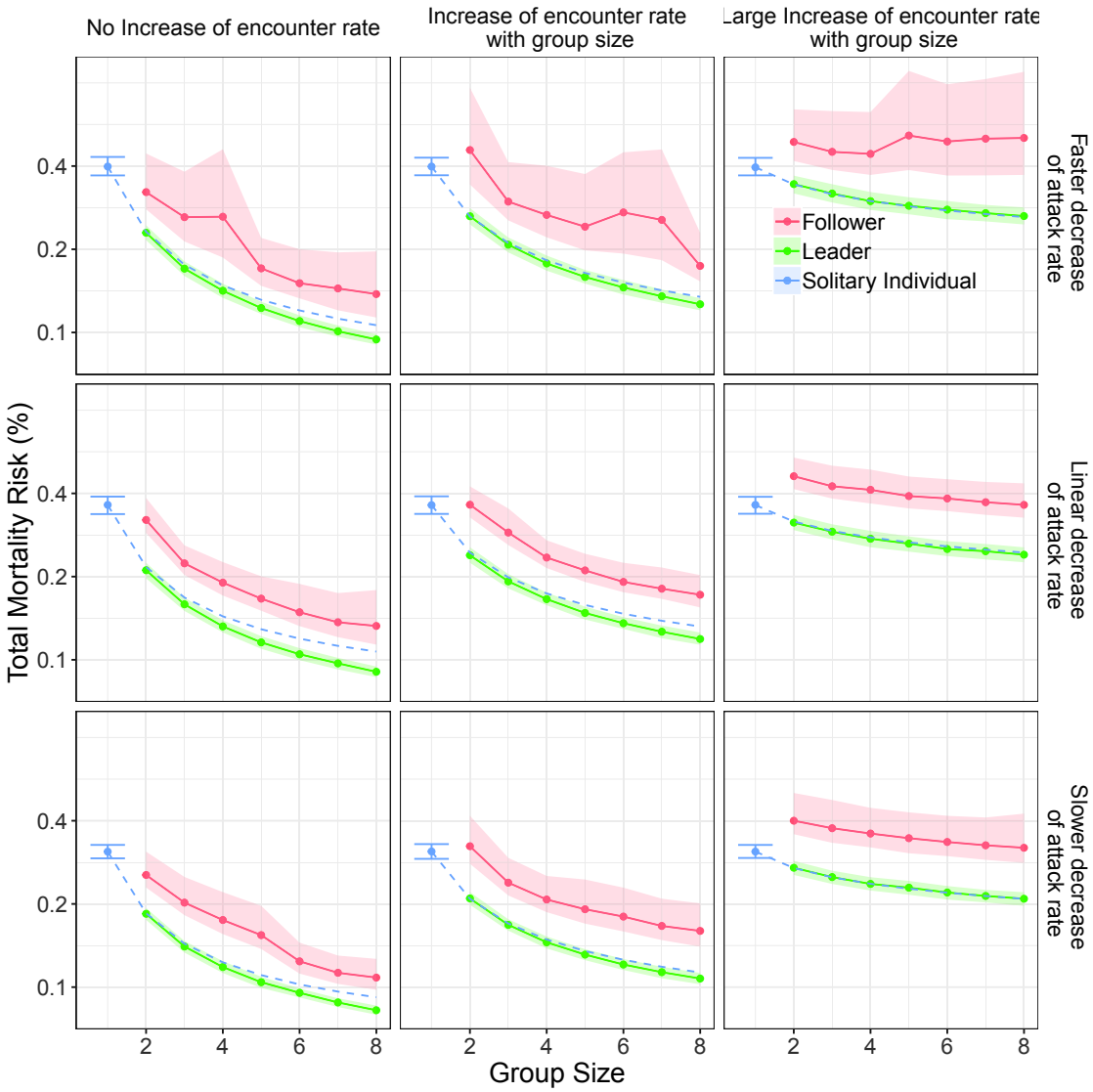


Figure S4-9 – Relationship between mean suffered mortality risk (%, median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator does not change ($k_2 = 0$, left), increases slightly ($k_2 = 0.25$, middle) or largely ($k_2 = 0.75$, right) with group size and attack rate deacreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance. Dashed lines show mortality risk of a leader that would adopt the optimal behaviour of a solitary individual. Percentages correspond to probabilities of death per simulation time step.



Supplement S5. Results from simulations of followers that maximized their short-term survival

To estimate the optimal strategy of followers maximizing their long-term survival, we had to make the assumptions that followers, even if they had no information about when they would leave a patch, knew what the long-term rate of patch leaving was. Said differently, they knew what the optimal strategy of the leader was. An alternative approach would be to assume that, in the face of uncertainties about space use decisions, followers maximize their short-term survival (i.e. their survival until the next time-step). In this case their life expectancy was really low (figure S5-3), because these strategies were leading to higher vigilance level. Vigilance of followers was then a lot higher, than the one of the leader (figure S5-1), which contrasted with results obtained under the assumption of followers knowing the long-term patch leaving rates (see figure 1 in main text). Under the short-term maximisation assumption, followers traded-off long-term gain in survival for short-term gain in survival by increasing vigilance and decreasing predation risk. Followers that aim to maximize short term survival decrease their vigilance to increase their foraging at lower nutritional state than a long term maximizer. Thus, under the short-term maximization assumption, followers maintained a lower nutritional state (see figure S5-2) that made the individuals face higher risks of starvation and lower risk of predation, which led to a higher total mortality risk (see figure S5-3). Selection should therefore facilitate the evolution of cognitive mechanisms allowing to acquire knowledge about future space use. Understanding how this knowledge is acquired (learning, hard-wiring via selection) is an interesting issue. In line with work showing that despotic leadership is hardly viable (Sueur, 2012), this suggests that even despotic leaders could have interest in integrating the needs of the followers in its space use decisions, as the survival of the followers is an important driver of its own fitness through the dilution effect.

Figure S5-1 – Relationship between mean time spent vigilant accross patches (%, median, lower and upper quartile, in the upper panel) and group size for leader (green), solitary individual (blue) or followers maximizing either long-term (red) or short-term survival (purple) in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch.

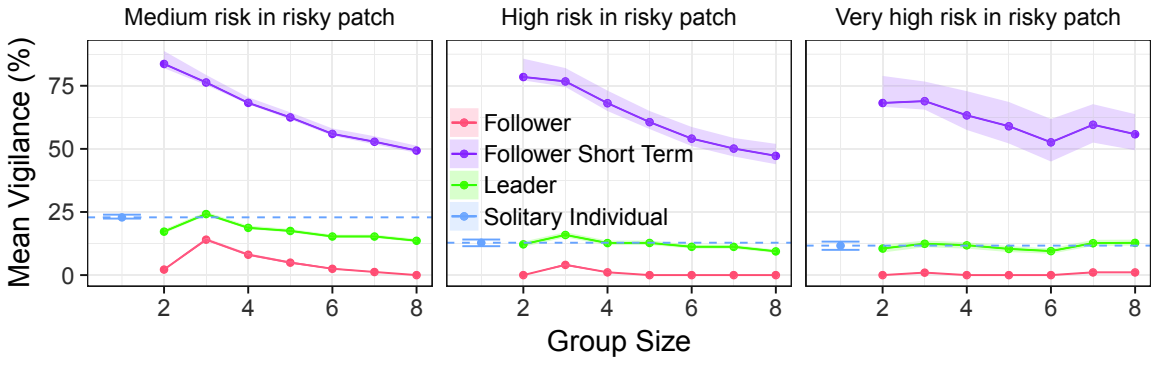


Figure S5-2 – Relationship between mean nutritional state (%, median, lower and upper quartile, in the upper panel) or standard deviation of nutritional state (%, lower panel) and group size for leader (green), solitary individual (blue) or followers maximizing either long-term (red) or short-term survival (purple) in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch.

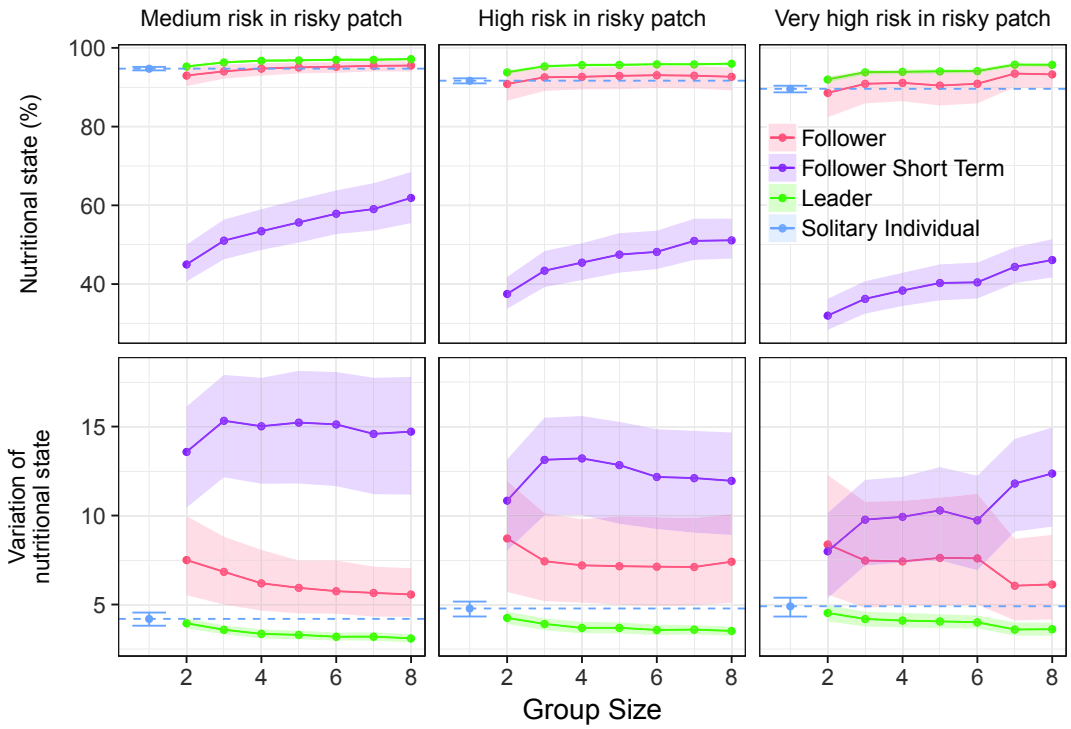
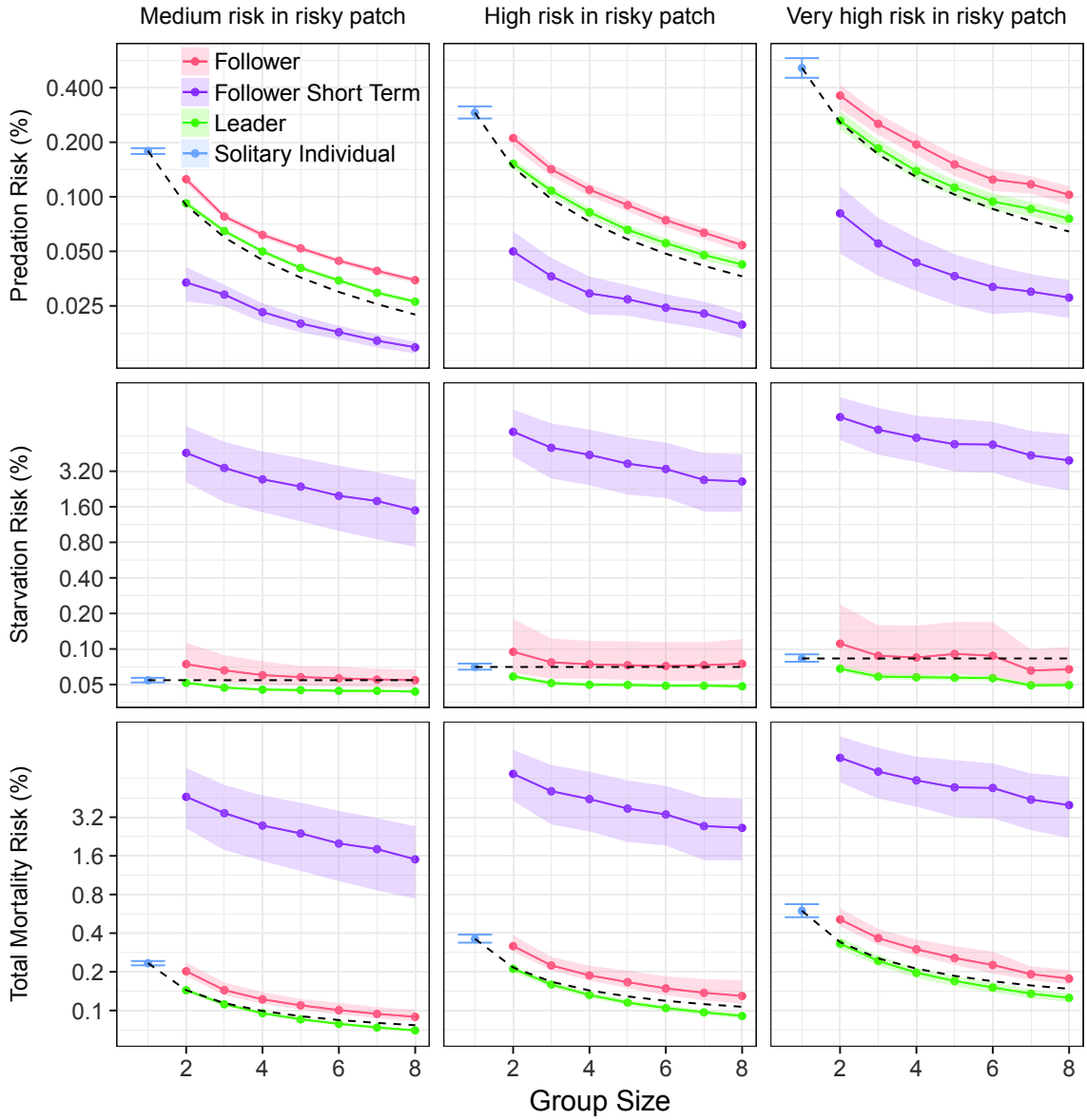


Figure S5-3 – Relationship between mean suffered predation risk (%, median, lower and upper quartile, in the upper panel), mean suffered starvation risk (%, medium panel) or mean suffered total risk (%, lower panel) and group size for leader (green), solitary individual (blue) or followers maximizing either long-term (red) or short-term survival (purple) in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch. Dashed lines show risk for a leader that would adopt the optimal behaviour of a solitary individual. Percentages correspond to probabilities of death per simulation time step.



Group-size effect on predation-driven space-use in plain zebra

Effet de la taille de groupe sur l'ajustement spatial au risque de prédation chez le zèbre des plaines (*Equus quagga*)

Rémi Patin, Camille Vitet, Daniel Fortin, Simon Chamaillé-Jammes

Analyses complémentaires

Abstract

Living in groups provides several benefits against predation. Individuals living in groups could benefit from an increased detection rate of predators, as well as a dilution of risk, each individual being less likely to be targeted by a predator when in a group. Those safety benefits explain why vigilance is often observed to decrease with group size : individuals in groups have less interest in decreasing their foraging rate for an increased vigilance. Such group-size effect could also affect any other anti-predator behavior. In this analysis, we focused on space use behaviour and tested whether larger groups used riskier areas of the landscape. We used GPS data of plains zebra (Equus quagga) living in groups of known size, and used lion GPS data to build a predictive map of where encounters with lions were most likely. Although we questioned the robustness of the results, they appear to support the hypothesis that larger groups use riskier areas of the landscape.

Introduction

Predation is an important driver of evolution and prey present numerous antipredator behaviour (Lima and Dill 1990). For instance, prey can benefit from group living through attack abatement, with each individual becoming less likely to get targeted upon an attack (Krause and Ruxton 2002; Lehtonen and Jaatinen 2016). Prey may also benefiting from early detection that can deter attacks of predator due to vigilance (Rasa 1989), or from adaptive space-use, that can decrease the encounter rate with predator (Laundré 2010, Chapter 2). All those behaviors therefore provide safety benefits but also carry foraging costs : grouping can increase competition (Krause and Ruxton 2002), vigilance can decrease foraging efficiency (Fritz et al. 2002; Fortin et al. 2004b) and safer habitat generally provides fewer foraging opportunities (Cowlishaw 1997; Williams and Flaxman 2012). This balance between foraging and predation risk is commonly known as the food/safety trade-off (Abrahams and Dill 1989; Heithaus and Dill 2002). As this trade-off is controlled by several behaviours, there is a potential for interactions among those (Lind and Cresswell 2005, Chapitre 1). Such a well known interaction is the dilution effect on vigilance (Lima 1995; Beauchamp 2013), when vigilance decreases as group size increases. This happens when the costs of grouping are lower than the foraging benefit of reduced vigilance. The increase in predation risk due to decreased vigilance is then compensated by the larger group size.

In the same way, we also expect grouping to interact with space-use (Chapitre 1). Several mechanisms can lead to a spatial food/safety trade-off : depletion of safer area because of increased prey use ; spatial game between predator and prey where predator benefits from matching the prey resources rather than the distribution of the prey themselves Williams and Flaxman (2012); Sih (2005). In any case, prey generally face a choice between risky and rich or safe and poor areas. With larger group size, prey could increase their use of the risky and rich areas, which would give foraging benefit. This increased use of risky habitat is then compensated by attack abatement. On the one hand, some observations have already shown that animals aggregate into larger groups in risky places (Barja and Rosellini 2008; Creel et al. 2014), but as risky places are sometimes linked to open habitat (Creel et al. 2014), this could be due to classical fusion-fission processes, as fusion rates increase with visibility (Gerard and Loisel 1995; Pays et al. 2007). Moreover, even if such grouping is a response to predation, its dynamic does not allow to study long-term consequences of grouping on the management of the food/safety trade-off. Highlighting such consequences would require following , over the long-term, the size of groups for given individuals, a difficult task when groups are highly dynamics. Williams et al. (2003) have experimentally found that larger coveys of bobwhite (*Colinus virginianus*) spent more time in risky open habitat. In their study, however, habitat is binary and the alternative is to find cover, in a refuge without food available, a simple situation that cannot represent the complex spatial distribution of food and risk that prey generally face.

In this study, we propose to test whether increasing group-size can lead to long-term riskier space use in a social species in a system with a complex distribution of predation risk. We will use data from plains zebra (*Equus quagga*), a species forming long-term

stable groups (Rubenstein 1986) and known to have strong spatial response to predation risk (see Chapter 2). Indeed, previous studies have found that in Hwange National Park, zebras perform diel migrations to and from waterholes to decrease encounter rate with lions (*Panthera leo*), their main predator (see Chapter 2). Zebras spend the day around waterholes in grassland, their best foraging habitat, but at night they go away from the waterholes, around which lions are intensively hunting. Zebras forms relatively small groups (3 to 9 individuals in this population), so competition and encounter rate with predator should not change much with group size on this gradient. Attack abatement, however, can potentially lead to threefold differences in predation risk : an individual in a group of 9 is 3 times less likely of being targeted by a predator upon attack, compared to an individual in a group of 3. This provides an opportunity to test interactions between anti-predator behaviours, in particular whether larger groups reinvest their safety benefits from attack abatement into a riskier space-use that should give foraging benefits.

Methods

The study was conducted in the north-eastern area of Hwange National Park, Zimbabwe. There are no perennial rivers at the study site, but about 30 pumped waterholes provide water all year round.

Thirty-four female zebras were collared with GPS loggers from 2008 to 2017, with data collection rate ranging from 30min to 6h. Plains zebras usually live in fixed group with one male, several females and their foals, yearling and related subadults. Data on group size for the GPS-collared zebra comes from both opportunistic observations (at the deployment or removal of collars for instance) and a demography study during which members of the zebra were identified and monitored twice a year from 2004-present (see Grange et al. 2015 for additional information). Group size data from the demography monitoring was used to verify that group size did not vary between two session if group composition was identical in the two instances. In instances, when we had a single observation session, we considered that group size did not change between one month before and one month after the observation. Group size was unlikely to change much over such short timescale.

We then subsampled the GPS fixes to keep day and night periods that had more than 6 location per period, along with information on group size. We removed individuals with data for less than 5 day or night periods. This gave us data from 23 individuals with 436 +/- 344 periods per individual (mean +/- sd). For each periods we calculated the predicted lion intensity of use, given a model that integrates season, time of day, habitat and distance to pumped waterhole (from Chapter 2).We calculated the mean predicted lion intensity of use over the period. We expected that predation risk would increase with group size at night, but would not be affected at day, because of lower predation risk during daytime hours. We also controlled for the potential presence of what could be seen as a refuge by zebras, the airstrip of the main camp of the park. Because of human activity in and near the camp during day and night, the airstrip is likely to be used less by large predators. If at least one of the period's location was inside the manually drawn polygon of the Airstrip

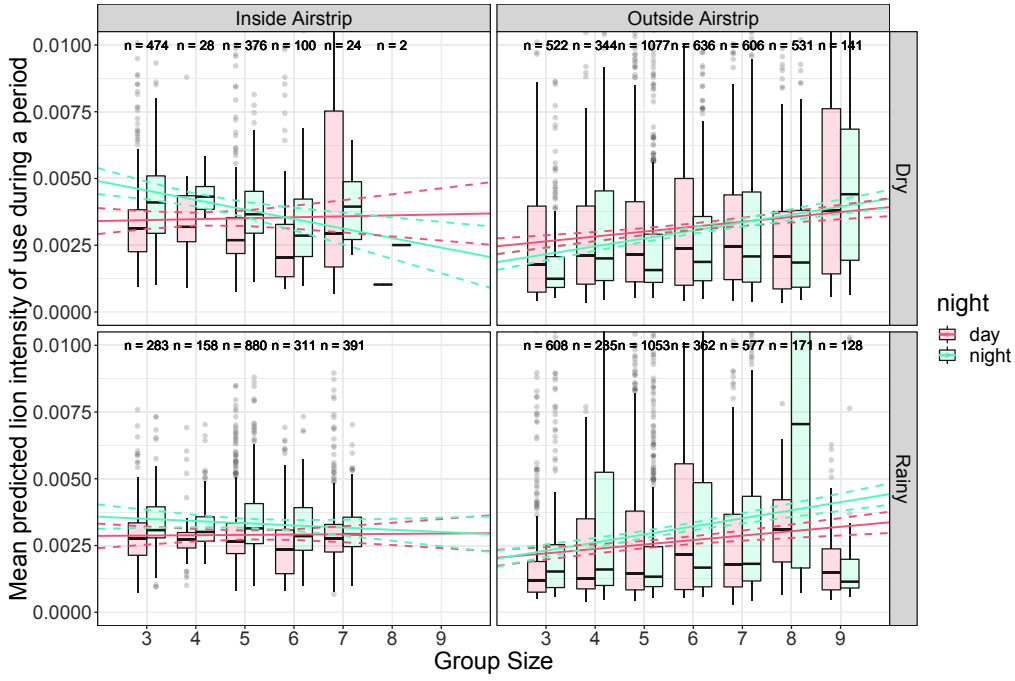
we classified the period as inside the Airstrip. We expected that in such context, the predation risk prediction may be biased and that there should be no response of predicted predation risk to group size.

To assess the significance of the relationship between group size and predicted lion intensity of use in areas used by zebras, we built a linear model whose response was the mean predicted lion intensity of use over the period with group size as a linear predictor and season, time of day (day or night) and whether or not any location was inside the Airstrip as interacting factors.

Results

For each combination of group-size, season, time of day and refuge availability that we could test we had 217+/- 170 periods (mean +/- standard deviation) corresponding to 4 +/- 2.3 different groups. Results suggest that outside the safer Airstrip area, larger groups of zebra use riskier areas more, supporting our main hypothesis (see fig. 1). For instance, a group of six individuals, that should theoretically suffer half the predation risk of a three individual group, has a space-use which is 40% riskier. Although smaller, the group-size effect is also significant during the day, occurs in both seasons. However, when groups foraged on the safer Airstrip area, larger groups did not use riskier areas, and possibly even use less risky areas, especially in the dry season.

FIGURE 1 – Mean predicted lion intensity of use over periods for zebra in groups of different size, for day and night (blue and red boxplots) in different season (dry season, upper part ; Rainy season, lower part) and for zebra within the safer Airstrip area (left panel) or outside (right panel). Horizontal line shows median. Box represent the first and third quartile. Whiskers are within 1.5 times the interquartile range of the first and third quartile.



Discussion

To our knowledge, this is the first example of group size effect on space use in stable groups. Our study shows that when zebra group size increases, groups tend to use riskier areas, confirming the dilution hypothesis. Larger groups, that decreased their per capita predation risk through attack abatement, took advantage of this decrease by foraging in riskier place. We also show that this behavior can be modulated when a refuge is available to the prey. Zebras near the Airstrip area did not display the same pattern of a riskier space-use with group-size. This group size effect on space use confirms that anti-predator responses may have important interactions that needs to be studied together (Lind and Cresswell 2005). In particular, when considering dilution effects on social species, space-use may be an important aspect for the prey's anti-predator strategy. We can also expect to see strong non-linear responses when vigilance, that commonly interact with group size, comes into play (see chapter 1).

A handful of previous studies have shown that larger groups were found in riskier places (Jarman 1974; Barja and Rosellini 2008; Creel et al. 2014). Such studies, however, are subject to bias, because larger groups can also be caused by the increased detection of conspecific in open and risky habitat (Gerard and Loisel 1995; Pays et al. 2007). Some studies looked at the influence of group size on decision making experimentally in very different taxa (fish : Krause et al. 2000 ; mosquito : Murthy et al. 2016) and empirically with American bison (*Bison bison*, Fortin et al. 2009). Krause et al. (2000) found that large stickleback in larger groups left refuges earlier, suggesting that grouping allowed a riskier space use. Murthy et al. (2016) found that larger groups of mosquito used the darker region of a petri dish, considered riskier, less. This was opposite to the expectation that larger groups would benefit to use riskier area as a consequence of risk dilution. Such study however did not use a real source of risk, but only assumed cue of risk, and was very short, not allowing to assess long-term changes in antipredator behaviours. Fortin et al. (2009) showed that larger groups of bison selected risky habitat more than smaller groups. By assessing both group fusion-fission dynamics and group movement this result was robust to the change in fusion rate in meadow and likely reflected consequences of risk dilution.

Conclusion

This exploratory analysis suggests an interesting pattern that would likely complete our current empirical (Fortin et al. 2009) and theoretical knowledge (Chapter 1) about the consequences of risk dilution on space-use. However, we considered these results not be robust enough (high noise, low number of locations and groups for some combination of factors) to continue these investigations and publish these results.

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Deuxième partie

CYCLE CIRCADIEN ET RISQUE DE PRÉDATION

Chapitre 2

Zebra diel migrations reduce encounter risk with lions at night

Les migrations quotidiennes permettent aux zèbres de réduire leur risque de rencontre avec les lions la nuit.

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Abstract

Diel migrations (DM; back and forth diel movements along an ecological gradient) undertaken by prey to avoid predators during the day have been demonstrated in many taxa in aquatic ecosystems. In terrestrial ecosystems, prey often shift between various vegetation types whose cover determine their vulnerability (i.e. likelihood of being killed when attacked).

We conceptualized that in terrestrial ecosystems DM could also occur, and that the contribution of DM and shifts in vegetation cover use in reducing predation risk should depend upon the predator behaviour and the correlation between encounter risk and vulnerability across vegetation types. We further hypothesized that when the predator distribution is predictable, terrestrial prey could have evolved DM strategies taking them away from the predator when it is active or efficient.

We investigated whether plains zebras (*Equus quagga*) perform DM in Hwange National Park (Zimbabwe). There, zebras can forage in large patches of open grasslands located near waterholes where they can also easily detect predators. However, they are there at high risk of encountering their main predator, lions (*Panthera leo*), especially at night.

We found out that zebras employ a DM anti-predator strategy. Zebras forage near waterholes during the day but move away from them at sunset, when lions become active. We demonstrated that this DM, occurring over a few kilometres, dramatically reduces their nighttime risk of encountering lions, which generally remain close to waterholes. Zebra changes in nighttime selection for vegetation cover types reduced their risk of encountering lions much less. This may arise from a trade-off between encounter risk and vulnerability across vegetation types, with zebras favouring low vulnerability once DM has reduced encounter risk.

In summary, here we (1) quantify, in a terrestrial system, the effect of a predator-induced DM on the likelihood of encountering a predator, and (2) distinguish the effects of the DM on encounter risk from those related to day/night changes in selection for vegetation types. We discuss how prey partition their risk between encounter risk and habitat-driven vulnerability and why it is likely critical to understand the emergence of anti-predator behavioural strategies.

Contents

1 Introduction

Predation is a pervasive evolutionary force that shape organisms behaviour (Lima and Dill 1990; Caro 2005). Most anti-predator behavioural responses are however balanced against other fitness-beneficial activities, in particular food resource acquisition (Lima and Dill 1990; Brown and Kotler 2004). Such food/safety trade-offs are central in predicting that prey, rather than minimizing predation risk, should have evolved finely-tuned behavioural strategies to best use their environments, adjusting dynamically to spatio-temporal changes in resources and predation risk.

A clear example of such adjustments is the relocation undertaken by many prey species between day and night periods. The hunting efficiency of predators often varies with light intensity, leading them to have well-defined, restricted windows of hunting activity during the 24h cycle (Clark and Levy 1988; Lima and Dill 1990; Kronfeld-Schor and Dayan 2003; Kohl et al. 2018). Prey thus experience alternating safer and riskier times, and may optimize their daily balance between forage acquisition and predation risk avoidance by making strategic use of rich resource areas when predators are inefficient and less active, while retreating to safer places during risky times (Fischhoff et al. 2007b; Middleton et al. 2013; Basille et al. 2015; Padié et al. 2015; Kohl et al. 2018). Such dynamical adjustments in prey space use over the diel cycle could have implications for non-consumptive effects of predators and trophic cascades (Kohl et al. 2018).

In terrestrial ecosystems, prey often relocate themselves in different vegetation types between day and night. Vegetation cover is a strong determinant of predators hunting efficiency (Mysterud and Østbye 1999; Hopcraft et al. 2005; Wirsing et al. 2010), and prey may use these diel shifts in habitat selection to reach habitats where they are less vulnerable (i.e., have a lower likelihood of being killed if attacked). These diel habitat shifts are widely observed, and could be particularly important when prey face predators such as wolves Canis lupus, whose space use at the landscape scale is poorly predictable (Creel et al. 2005; Middleton et al. 2013; Basille et al. 2015; Schmidt and Kuijper 2015; Kittle et al. 2017). When prey face predators with a predictable space use (i.e., when predators focus on prey resource patches rather than on tracking prey themselves; Sih 2005), prey may also reduce their encounter risk by moving away from risky areas during the active periods of the predator. Such strategy would lead to diel migrations (hereafter, DM), defined as back and forth movements along a spatial, ecologically relevant, gradient. For instance, along a gradient of predation risk, prey would move away from spatially risky areas during the risky periods and move back to these risky areas when it becomes safer. There are surprisingly few examples of DM in terrestrial systems, except in the context of human hunting with hunted species moving to protected areas during the day (Tolon et al. 2009; Fortin et al. 2015). Conversely, DMs have been commonly described in a wide range of taxa in aquatic ecosystems (Alonzo et al. 2003; Hays 2003; Benoit-Bird and Au 2006). For example, in marine systems, zooplankton forage on phytoplankton at the sea surface at night when their predators have a reduced visual acuity, and move towards deeper water during the day to reduce the risk of being detected, leading to the emergence of diel vertical migrations (Iwasa et al. 1981; Hays 2003). In these systems, the DM takes prey not only significantly away from the predators during the risky periods but also to areas where these predators are less efficient (the predator evasion hypothesis; Hays 2003). Thus, DM in aquatic ecosystems cannot shed light on whether prey would, in the pres-

ence of predictable predators, evolve DM strategies, irrespectively of their potential effect on vulnerability.

Here, we tested in a terrestrial ecosystem the hypothesis that prey develop a DM strategy when confronted with a primarily nocturnal predator whose distribution is predictable and spatially anchored near prey resource patches. We focused on the diel space use patterns of African lions Panthera leo and plains zebras Equus quagga, in Hwange National Park (hereafter Hwange NP), Zimbabwe. In HNP, zebra is one of the five main prey species of lions (Davidson et al. 2013), and lion is the main predator of zebras (pers. obs.). In this mostly wooded savannah ecosystem, artificial waterholes are associated with large open areas (Chamaillé-Jammes et al. 2009a; Courbin et al. 2016), which are rare (<2% of the study area), and the abundance of large herbivores is high in these areas, which can be considered prey hotspots. Zebras favour these short-grasslands during daytime (Valeix et al. 2009; Courbin et al. 2016) as they provide profitable forage and high visibility. Lions are ambush predators that need vegetation cover to approach their prey undetected and launch a successful attack (Loarie et al. 2013). However, in HNP, lions search for prey in grasslands near waterholes at night (Valeix et al. 2010; Davidson et al. 2013; Courbin et al. 2016). We therefore predicted that zebras should display DM, coming close to waterholes during the day to forage when lions are less active, and moving away at night to decrease the risk of encountering lions when they become active. Our results supported this prediction. We then quantified to what extent the DM of zebras decreased their risk of encountering lions. Given the lion distribution focused around waterholes, we predicted that the effect of DM on encounter risk should outweigh those of potential diel changes in the use of vegetation cover types.

2 Materials and methods

2.1 Study site

The study was conducted in Hwange NP, Zimbabwe. The vegetation is typical of dystrophic semi-arid wooded savannahs (average annual rainfall is c. 600 mm), with woodlands and bushlands interspersed with small grassland patches (Chamaille-Jammes et al. 2006). We focused on two contrasting seasons: the wet season (November to April) and the late dry season (August to October). During the latter, zebras drink at artificial waterholes (hereafter referred to as 'waterholes') that are the only perennial sources of water. All statistical analyses were conducted for both seasons. In the study area, zebras make up <10% of the lion diet (Davidson et al. 2013). Lion population density is however high at c. 3.5 lions/100 km2 (Loveridge et al. 2016) and predation likely controls the zebra population (Grange et al. 2015), which is currently stable or slightly declining at c. 100 zebra/100km2 (Chamaillé-Jammes et al. 2009b; Grange et al. 2015, unpublished demographic data).

2.2 Testing for the existence of zebra DM

We used GPS locations collected hourly from 25 adult female zebras (18 zebras in dry season and 24 zebras in wet season), collared in different herds between August 2009 and November 2013, to assess if zebras moved away from waterholes at night. For each day and night of each season, we estimated the distance to the closest waterhole (hereafter 'distance to waterhole') as the median of the distances to a waterhole an individual was over its GPS locations for the given day or night. See Appendix S1: fig. S1.1, for the sunrise/sunset-based definition of day/night periods.

We used least-squares spectral fitting to test that distance to waterhole displayed a 24h-periodicity. For each zebra in each season, we visually inspected Lomb-Scargle periodograms (Ruf 1999) for peaks around 24h, and tested the significance of the largest peak within the 20 to 28h window using the randomization procedure implemented in the lomb package (Ruf 1999) for the R software(R Core Team 2016). For individuals displaying a significant 24h-periodicity in distance to waterhole (i.e. those performing a diel migration), we investigated if displacement away from waterholes depended upon their proximity to waterholes during the previous daytime period. We did this by modelling the relationship between the nighttime movement away from waterholes and the distance to waterhole during the preceding day using a generalized additive mixed model (GAMM) with thin plate regression splines (Wood and Scheipl 2017). Individuals were included as random factors to account for non-independence of GPS locations within an individual. The model was fitted using the gamm4 package (Wood and Scheipl 2017) for the R software (R Core Team 2016).

2.3 Modelling the risk of encountering lions in the landscape

We first used GPS data from lions, collected over the same period as for zebras, and inhomogeneous Poisson point process models (Aarts et al. 2013; Johnson et al. 2013) to build predictive maps of the risk of encountering lions across the landscape (see Appendix S2). Separate risk maps were built for daytime and nighttime because lions displayed day/night changes in habitat selection (see fig. 1 and Appendix S2: table S2.2). We validated the predictive performance of our daytime and nighttime risk maps using the k-fold cross validation method (Boyce et al. 2002).

2.4 Quantifying the relative effects of DM and changes in use of vegetation cover on the risk of encountering lions

To disentangle the relative effects of DM and changes in selection for cover at night in decreasing the risk of encounter between zebras and lions, we estimated and compared the actual risk experienced by zebras during the daytime and nighttime situations (situations 1 and 2 respectively) and two hypothetical situations reflecting either a lack of behavioural adjustments of zebras at night (situation 3 whereby zebras do not move away from waterholes and do not alter their selection for vegetation cover type), or the use of DM only, without changes in the use of vegetation cover at night (situation 4). We combined zebra GPS locations and encounter risk maps (section Modelling the risk of encountering lions in the landscape), and for each situation we estimated risk experienced by zebras as follow:

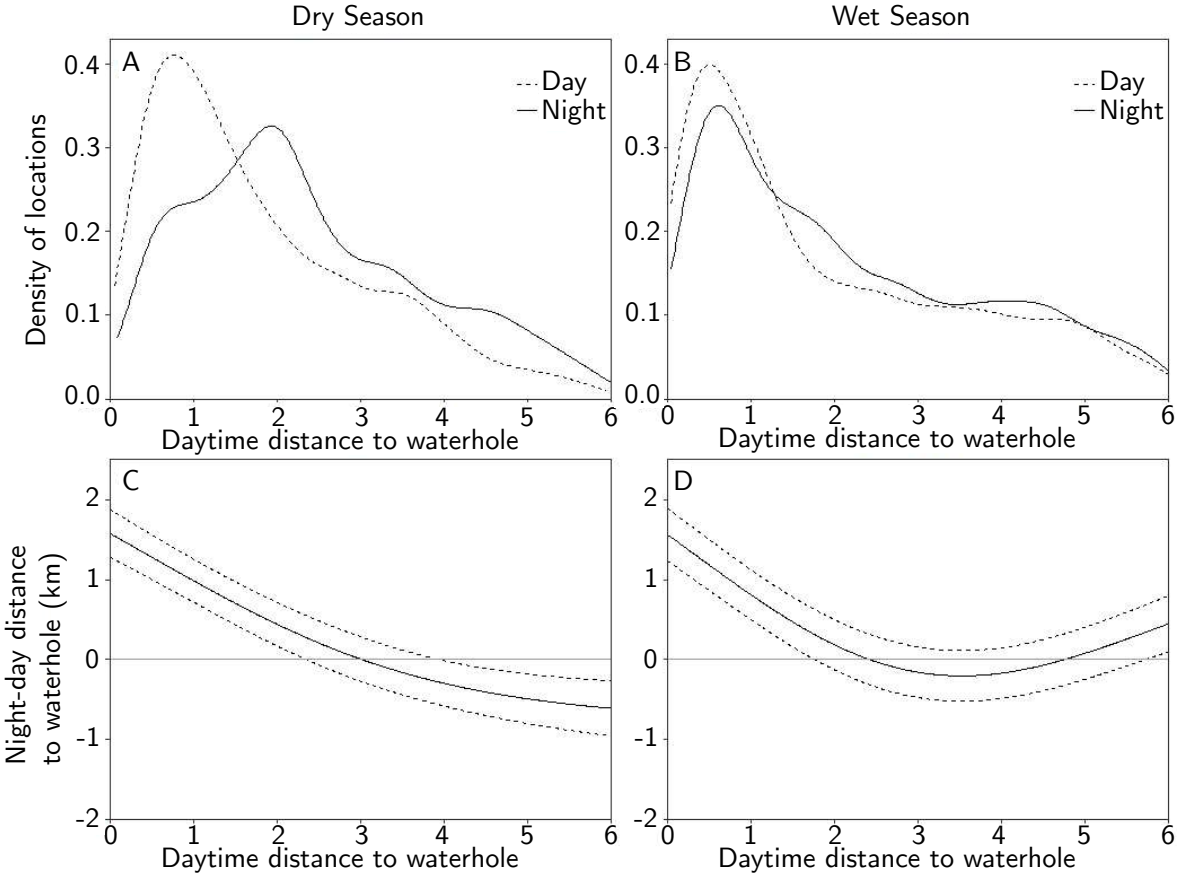
- Situation 1, *"actual zebra daytime risk"*: we estimated zebra risk of encountering lions during the day by extracting, for each zebra GPS location acquired during daytime, the risk of encountering lions from the daytime risk map, and calculated the median risk over each day.
- Situation 2, *"actual zebra nighttime risk"*: we estimated zebra risk of encountering lions during the night by extracting, for each zebra GPS location acquired during nighttime, the risk of encountering lions from the nighttime risk map, and calculated the median risk over each night.
- Situation 3, *"hypothetical zebra nighttime risk in absence of behavioural adjustments"*: for this hypothetical situation, we assumed that zebras neither moved away from waterholes nor altered their selection for vegetation cover type at night. To calculate risk, we considered that, for each night, zebra GPS locations were those of the preceding daytime period (i.e. the use of vegetation types and distance to waterhole were thus retained). We then extracted the risk of encountering lions from the nighttime risk map, and calculated the median risk over each night.
- Situation 4, *"hypothetical zebra nighttime risk with DM only"*: for this hypothetical situation, we assumed that at night zebras used the various vegetation types exactly as during the preceding daytime period, but adjusted their distance to waterhole. To calculate risk, we considered that, for each night, zebra GPS locations were those of the preceding daytime period (i.e. the use of vegetation types was thus retained), but that their distance to waterhole was shifted by a distance equal to the particular observed diel migration between this night and the preceding daytime period (i.e., the difference between the median distance to waterhole over the actual nighttime GPS locations and the median distance to waterhole over the GPS locations of the preceding daytime period). Then, for each zebra GPS location, we extracted the risk of encountering lions from the nighttime risk map, and calculated the median risk over each night.

We compared these situations to estimate the changes in risk levels experienced by zebras and quantify the contribution of the various behavioural adjustments underlying these changes. We compared situation 1 (actual daytime risk) and situation 3 (hypothetical nighttime risk in absence of zebra behavioural adjustments) to estimate to what extent lion behavioural changes at night would increase zebra risk of encountering lions if zebras behaved as they did during the day. We compared situation 2 (actual nighttime risk) and situation 3 (hypothetical nighttime risk in absence of zebra behavioural adjustments) to estimate to what extent zebra behavioural changes at night (i.e., changes in selection for vegetation types and DM) reduced their risk of encountering lions. We compared situation 3 (hypothetical nighttime risk in absence of zebra behavioural adjustments) and situation 4 (hypothetical zebra nighttime risk with DM only) to estimate to what extent DM only decreased encounter risk at night. Finally, we compared situation 2 (actual nighttime risk) and situation 4 (hypothetical zebra nighttime risk with DM only) to estimate the extent to which changes in vegetation cover types used reduced encounter risk.

Statistical analyses were conducted by fitting a linear mixed model, with the response variable containing the risk values for each day (situation 1) or night (situations 2, 3, 4), and the predictor coding the situation. We used random intercepts for individual IDs to consider the non-independence among multiple periods for each individual. From this model, we obtained both estimates of the mean risk value and the associated 95% confidence intervals for each situation (no intercept model) and estimates of differences in

risk between situations (model with intercept). Models were fitted using the lme4 package (Bates et al. 2014) for the R software (R Core Team 2016).

Figure 1 – (A, C) Distribution of zebra locations as a function of distance to waterhole during daytime and nighttime. The distribution is truncated at 6km (dry season: for both day and night 90% of data are shown and the tail reaches c. 15km; wet season: 76% and 78% of daytime and nighttime data are shown, respectively, the tails of the distribution reach 38km [daytime] and 34km [nighttime]). (B, D) Difference between zebra distance to waterhole at night and their distance to waterhole during the previous day, as predicted by a generalized additive mixed model (dry season: df=2.827, F=119.8, P<0.001; wet season: df=2.986, F=134, P<0.001). Positive (negative) values indicate that zebras moved away from (closer to) waterhole at night. Dotted lines represent the 95% confidence interval.



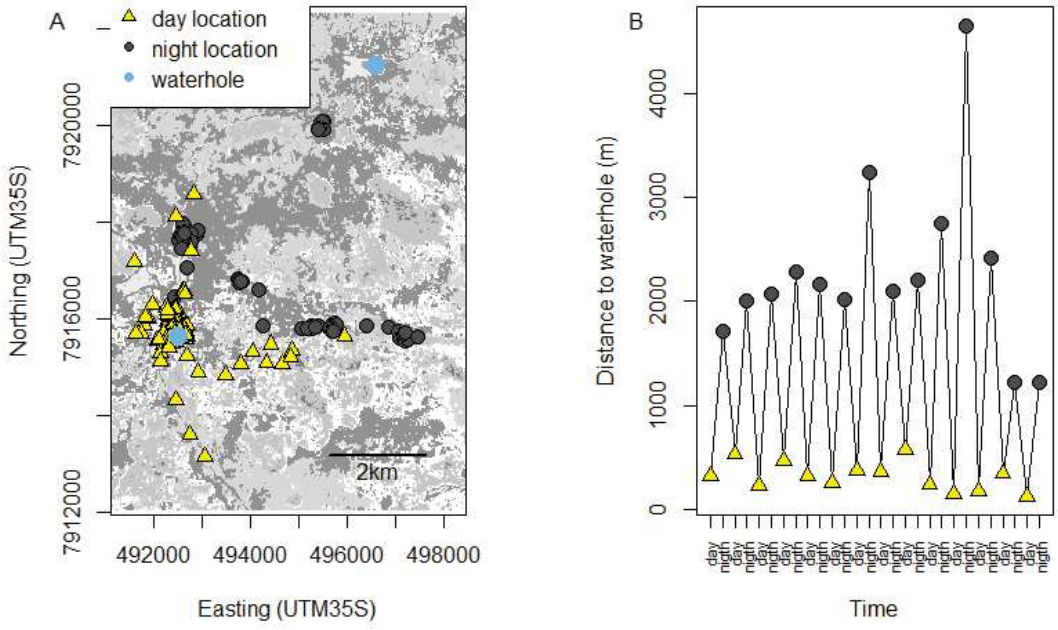
3 Results

3.1 Zebras undertake DM

During the dry season, zebras were generally within a few kilometres of a waterhole, but were closer to waterholes during the day than at night (figs 1A, 2). Periodogram analyses confirmed that distance to waterhole displayed a well-marked 24h cycle that was significant for 83% of the individuals, while DM frequency varied among individuals (note the variability in normalized power values, fig. 3A). Zebras moved towards waterholes in the first hours of the morning and moved away at sunset (see Appendix S1: fig. S1.1). For zebras with a significant DM pattern, the magnitude of DM declined as daytime distance to waterhole increased, the estimated DM being up to 1.7 km when zebras were in the close proximity of a waterhole during the day (fig. 1B). No DM occurred beyond a daytime distance of 2.4 km. Zebras possibly even moved towards waterholes at night when > 4 km from them during the day, although the magnitude of DM was small and kept zebras at intermediate distance to waterholes at night (fig. 1B).

During the wet season, zebras remained close to waterholes at night more often than during the dry season (fig. 1C). Zebras also used DM but, compared to the dry season the 24h-periodicity in back-and-forth movement to waterholes was significant for a lower proportion of zebras (54%) and DMs were less frequent (i.e., lower normalized power values, fig. 3B). Also, for zebras with a significant DM pattern, the DM vanished at shorter daytime distance to waterhole (1.8 km, fig. 1D).

Figure 2 – Example of diel migration behaviour. The panels display (A) GPS locations and (B) the median distance to the closest waterhole during day and night, using data obtained from zebra ID AU299 over a 14-day period during the 2009 dry season in the Hwange National Park, Zimbabwe.



3.2 Relative importance of zebra behaviours in reducing encounter risk with lions

During the dry season, the risk of encountering lions, as indexed by our models of lion habitat selection, always decreased rapidly with the distance to waterhole, and increased with vegetation openness, especially at night (Appendix S2: fig. S2.1 and Table S2.2). This would lead zebras to experience a 160% increase in risk at night if they did not adjust their behaviour ($\text{risk}_{\text{situation 3 (hypothetical nighttime risk in absence of behavioural adjustments)}}$ [mean (95% CI): 1.16 (0.96;1.37)] > $\text{risk}_{\text{situation 1 (actual daytime risk)}}$ [0.72 (0.47;0.92)], $P < 0.001$; fig. 4). The DM undertaken by zebras allowed them to largely reduce their risk of encountering lions at night ($\text{risk}_{\text{situation 4 (hypothetical nighttime risk with DM only)}}$ [0.86 (0.64;1.05)] < $\text{risk}_{\text{situation 3 (hypothetical nighttime risk in absence of behavioural adjustments)}}$, $P < 0.001$, fig. 4). Quantitatively, the relative contribution of DM in decreasing zebra nighttime encounter risk with lions was of 90% $\left(\frac{\text{risk}_{\text{situation3}} - \text{risk}_{\text{situation4}}}{\text{risk}_{\text{situation3}} - \text{risk}_{\text{situation2}}} \times 100\right)$, while changes in vegetation types used by zebras at night contributed for 10% only $\left(1 - \frac{\text{risk}_{\text{situation3}} - \text{risk}_{\text{situation4}}}{\text{risk}_{\text{situation3}} - \text{risk}_{\text{situation2}}} \times 100\right)$. Consistently, we did not find empirical support that changes in vegetation types used by zebras at night decreased their nighttime encounter risk with lions ($\text{risk}_{\text{situation 2 (actual nighttime risk)}}$ [0.83 (0.69;0.96)] did not differ significantly from $\text{risk}_{\text{situation 4 (hypothetical nighttime risk with DM only)}}$), $P > 0.10$, fig. 4).

During the wet season, patterns were broadly similar (figs 1D, 4), but zebras generally stayed closer to waterholes and DM were shorter when they occurred (figs 1C, D). Consequently, zebra risk of encountering lions was generally larger for all situations, and the reductions in encounter risk were smaller. The relative contribution of DM in decreasing nighttime encounter risk was of 58% $\left(\frac{\text{risk}_{\text{situation3}} - \text{risk}_{\text{situation4}}}{\text{risk}_{\text{situation3}} - \text{risk}_{\text{situation2}}} \times 100\right)$ while changes in vegetation types use at night contributed for 42% $\left(1 - \frac{\text{risk}_{\text{situation3}} - \text{risk}_{\text{situation4}}}{\text{risk}_{\text{situation3}} - \text{risk}_{\text{situation2}}} \times 100\right)$ in decreasing encounter risk (fig. 4). The lower contribution of DM to the reduction in risk, compared to the one observed in the dry season, was likely due to the fact that lions are more spread away from waterholes in the wet season (Appendix 2, fig. S2.1).

Figure 3 – Periodograms of the distance to waterhole time-series for (A) the dry season and (B) the wet season. Each line represents the periodogram for one individual zebra, and the maximum value of each periodogram spectrum within the 20 to 28h-period window is indicated by a triangle. Black triangles pointing up and grey triangles pointing down indicate significant (P<0.05) and non-significant (P± 0.05) peak values, respectively. Peak values were significant for 83% (15 out of 18) of the individuals in the dry season, and for 54% (13 out of 24) of the individuals in the wet season.

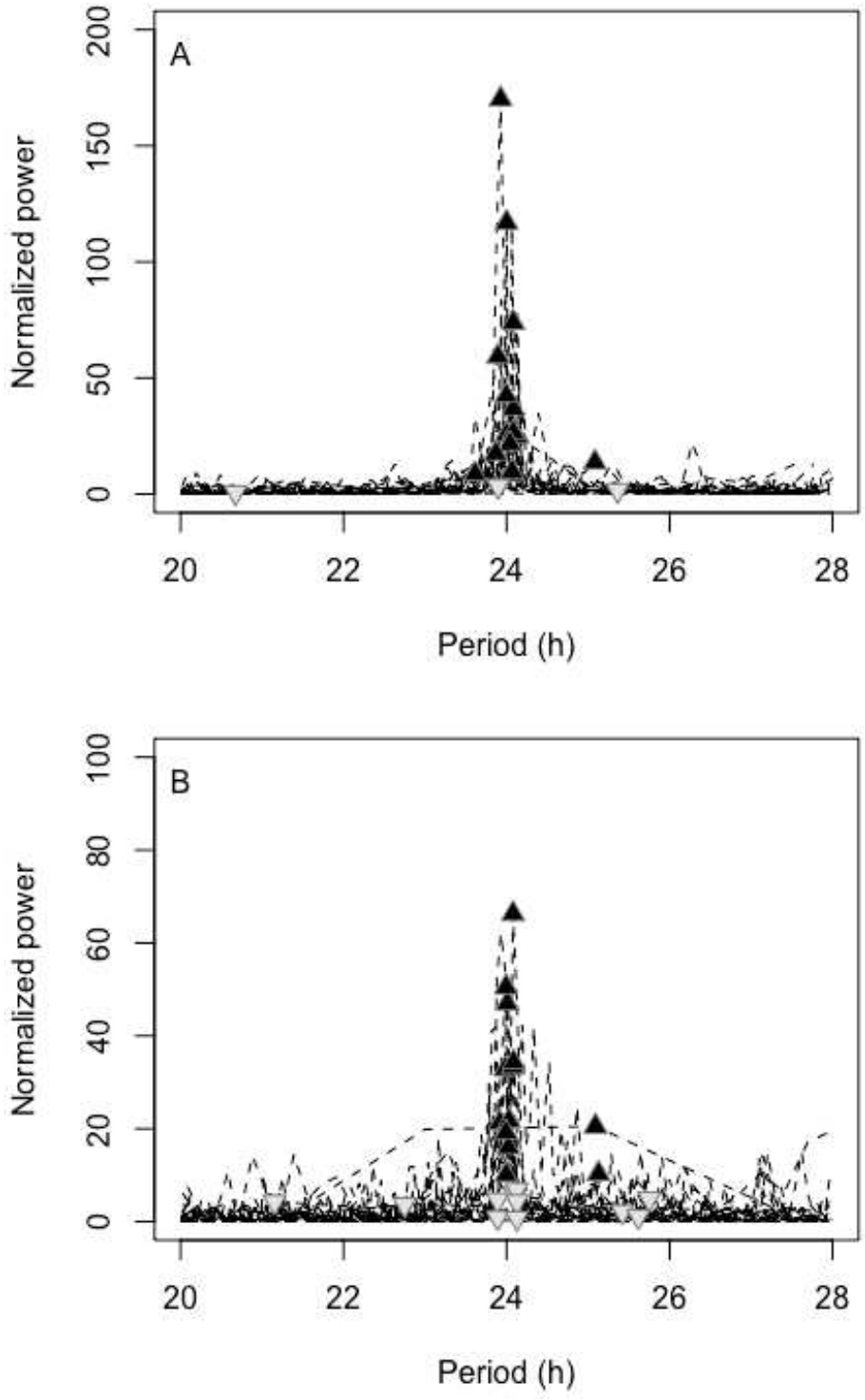
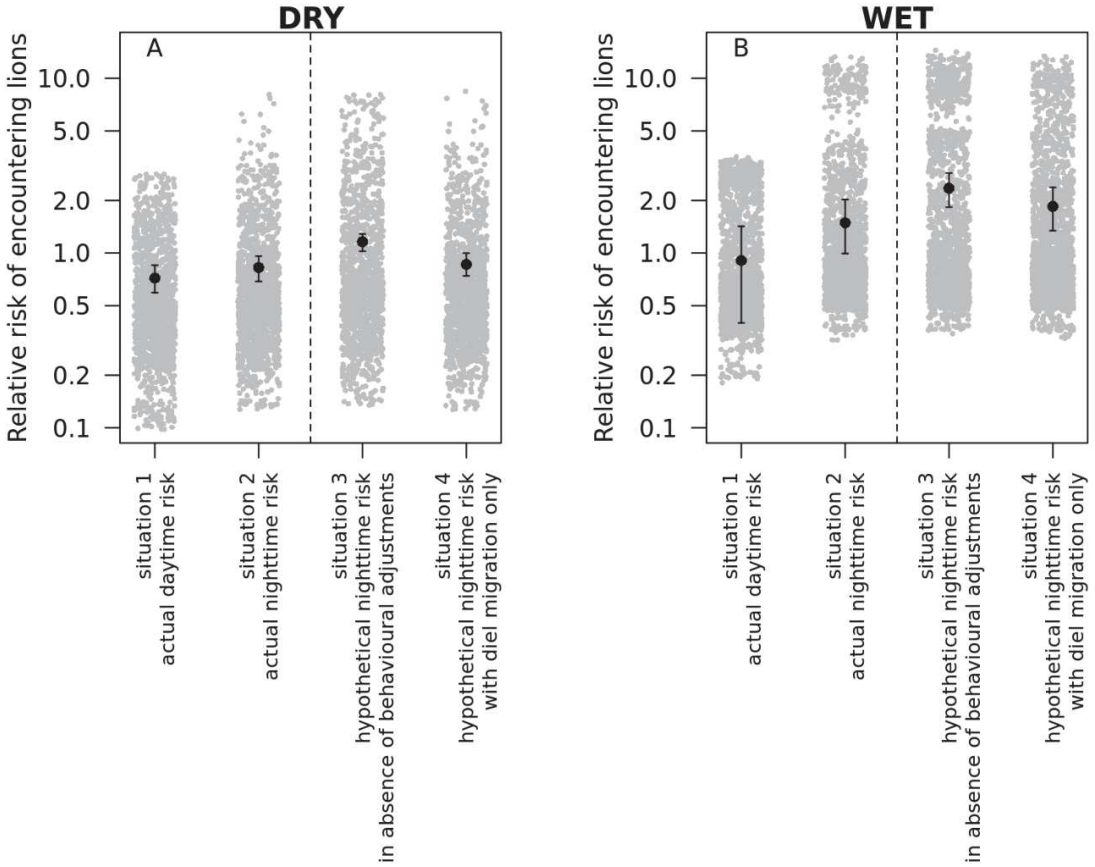


Figure 4 – Expected risk of encountering lions for zebras during the dry (A) and wet (B) seasons, in four situations: actual daytime risk (situation 1), actual nighttime risk (situation 2), hypothetical nighttime risk in absence of behavioural adjustments of zebras (no DM and no change in selection for vegetation types) (situation 3), hypothetical nighttime risk with zebra diel migration but unchanged zebra use of the different vegetation cover types (situation 4). The actual risk situations were separated from the hypothetical risk situations with a dotted line. Risk is shown on a log scale. All possible comparisons are significant at alpha = 0.05 for each season, except between situations 2 and 4 in the dry season. See the Results section for details.



4 Discussion

Our study shows that, in Hwange NP, zebras use areas located near artificial waterholes during daytime, benefiting from the large open grasslands (Chamaillé-Jammes et al. 2009a; Courbin et al. 2016), but routinely move away from them at risky night period, thereby reducing their risk of encountering lions. The diel cycle of predator-avoidance revealed here relies on diel migration and is independent of vegetation cover types, as at night zebras still use open grasslands (Courbin et al. 2016), conveying an alternative strategy to the well-known day/night habitat selection shift reported so far in terrestrial systems (Mysterud and Østbye 1999; Kronfeld-Schor and Dayan 2003; Laundré 2010). Also, the anti-predator diel migration occurring here or in aquatic systems (Iwasa et al. 1981; Burks et al. 2002; Hays 2003; Benoit-Bird and Au 2006), where prey can never be free of predation risk, differs from the diel response showed by hunted ungulates that take refuge during the day in protected areas completely free of risk (no hunting), e.g. wild boars (*Sus*

scrofa L.) (Tolon et al. 2009) and bison (*Bison bison*) (Fortin et al. 2015).

4.1 An alternative hypothesis unrelated to predation risk

Although our results are highly consistent with zebra diel migration being an anti-predator behaviour, we considered the alternative hypothesis that the zebra diel migration could be driven by a daily need to drink but also to forage in better places located far away from water, which could potentially be less depleted. Although we did not have data to test whether forage is more available or of higher quality further away from waterholes, we argue this hypothesis very unlikely. If it was beneficial to forage away from waterholes, we would expect zebras to minimize their time near waterholes, as found in other ecosystems where the best foraging places are located far from water (Cain et al. 2012). This is not what we observed, as during the day zebras stayed close to waterholes for much longer than what would be required to simply come and drink (which they would do in an hour or so, Périquet et al. 2010). When in open grasslands near waterholes, zebras are not only seen travelling, but mostly commonly are observed foraging or resting (Chamaillé-Jammes pers. obs.). Daytime preference of zebras for areas located near waterholes was also observed in Valeix et al. (2009), a study conducted in the same area but with different data. In addition, zebras would have no reasons to be near waterholes in the wet season when they do not need to drink. However, their attraction to areas near waterholes is more marked in the wet season than in the dry season. Generally, our results are not consistent with the hypothesis that zebras would prefer foraging away from waterholes. Results are more consistent with the hypothesis that nighttime avoidance of lions explains the diel migration of zebras away from their preferred foraging areas located near waterholes.

Diel migration is advantageous when space use of the predator is predictable Diel migration may emerge as an efficient strategy to deal with food/safety trade-offs when prey can reliably identify and travel to places where the absence of a predator is likely (Iwasa et al. 1981; Sainmont et al. 2013). This could in particular occur with ambush predators that focus around prey hotspots, and have multiple prey species to hunt, some being more spatially constrained that others. This creates an asymmetry by which the most mobile prey greatly benefit from moving away from these hotspot during the risky times, while the predator has little incentive to do so and engage in a costly search. In Hwange NP, lions remain near waterholes most of the time, despite being free to move anywhere (Valeix et al. 2010; Courbin et al. 2016, this study). The large patches of grasslands located near these waterholes attract grazers and mixed-feeders all year round, and the many water-dependent species naturally use these waterholes during the dry season. Lions, which can feed on a large number of species, do not need to track zebras moving away from waterhole areas if some other prey species remain near waterholes at night. This is the case of several large species (e.g. buffalo, *Syncerus caffer*; giraffe, *Giraffa camelopardalis*; elephant, *Loxodonta africana*) whose individuals are regularly seen drinking at night (Valeix et al. 2007), are killed close to water (Davidson et al. 2013), and make a dominant share of the lions' diet in Hwange NP (Davidson et al. 2013). Irrespective of why lions remain near waterhole areas, their behaviour makes areas away from waterholes predictably safer, and our results show that zebras benefit from this predictability. Zebras have developed a DM strategy allowing them to more than halve their risk of encountering lions at night, when lions hunt, compared to staying near waterholes. Thus, daily zebra movements to and

from waterholes may provide a mechanistic explanation for the low nighttime lion-zebra encounter rate observed in Hwange NP (one encounter every 35 days on average, Courbin et al. 2016).

Contrary to ambush predators such as lions, coursing predators such as wild dogs (*Lycaon pictus*) in African savannahs or wolves in temperate systems, roam over vast areas to locate suitable prey, and presence/absence of such predators could be less predictable. Prey of cursorial predators should therefore shift towards safer neighbouring habitats when the predator is detected or is likely to revisit the area rather than moving towards areas where predation risk is uncertain (Creel et al. 2005; Middleton et al. 2013; Latombe et al. 2014; Basille et al. 2015; Schmidt and Kuijper 2015; Kittle et al. 2017; Kohl et al. 2018, see examples with wolves).

Overall, the emergence of diel migration is closely linked to the landscape context constraining the spatial behaviour of predators (i.e. presence of a spatial anchor), and to the food web complexity (i.e., predator-multi-prey system) potentially relaxing the need for a predator to search for one prey species in particular. In this context, it would prove valuable to test the existence of DM in other prey and other ecosystems, contrasting situations with varying levels of prey and predator predictability.

Does the absence of safe vegetation types facilitate the emergence of DM? We found that zebras did not alter their selection for vegetation types at night to an extent that would significantly reduce encounter risk with lions. We suspect that this is due to a trade-off between encounter risk and vulnerability across vegetation types. At night, lions strongly select for more open vegetation, possibly to benefit from increased visibility and to maximize encounter rates with prey (Courbin et al. (2016); see Appendix S2: fig. S2.1). Zebras could reduce the risk of encountering lions by selecting for more bushy vegetation (see Appendix S2: fig. S2.1), but they would then become highly vulnerable in case of an encounter with lions which are primarily ambush/stalking predators (Caro 2005; Davidson et al. 2012; Loarie et al. 2013). Therefore, zebras may decrease encounter risk while maintaining a low vulnerability by conducting DM towards open vegetation types localized in relatively safe areas (i.e. far from waterholes).

Do DMs have population-level consequences? Our results could suggest that DM, which strongly decreases zebra likelihood of encountering lions, is a prime determinant of zebra survival rate. However, data from both lion kill surveys (Davidson et al. 2013) and zebra demographic monitoring (Grange et al. 2015) show that adult zebras are less likely to be predated upon by lions during the wet season, when we found that DMs were much less prevalent than in the dry season. It is yet unknown if this seasonal difference in DM patterns is driven by resources or predation sensitivity. It could be linked to the higher cost of leaving the best foraging patches at a time when grass quality is high. Also, it could be that lion favour other prey during the wet season, although previous work does not suggest so (Davidson et al. 2013). All these explanations could explain the lack of relationship between predation rate on adults and prevalence of the diel migration across seasons, but all remain speculative. Also, it is possible that in the wet season, during which most zebra foals are born, lions favour hunting juvenile zebras. Almost half of the juvenile zebras are killed during their first 6 months, mostly by lions (Grange et al. 2015). Therefore, the link between DM and adult predation rate may be distorted by the seasonal presence of juveniles. Groups with new-borns may be less mobile. However, the presence of juve-

niles, which are more vulnerable than adults, could actually increase the impetus for DM to reduce encounter rate. Overall, it remains to be investigated if individual variability in juvenile survival rate could be linked to the ability of some herds to perform longer DM earlier after the birth season. This would allow assessing the population-level consequences of DM, which may occur via consumptive or non-consumptive (e.g. increased energetic expenditure) effects.

5 Conclusion

The study of DM may thus help to clarify the respective roles of encounter risk and vulnerability in driving anti-predation behaviour. Our study emphasizes that DM could possibly be a more general anti-predator strategy than previously thought, and opens new research avenues to better understand the conditions under which it may evolve. In particular, it offers opportunities to study how the behaviour of the predator (i.e. mobility and hunting mode), the constraints for the prey (i.e. resource needs, presence of young) and the spatial context of their interactions (i.e. availability and spatial arrangement of the resource patches) determine the efficiency of DM compared to other anti-predator strategies. Generally, our study answers previous calls to consider the temporal patterns in the predator-prey space race (Hammond et al. 2007). Prey may use high risk, rich food patches during periods of predator inactivity or inefficiency, and move away from these patches when an encounter with the predator becomes more likely or dangerous.

Acknowledgements

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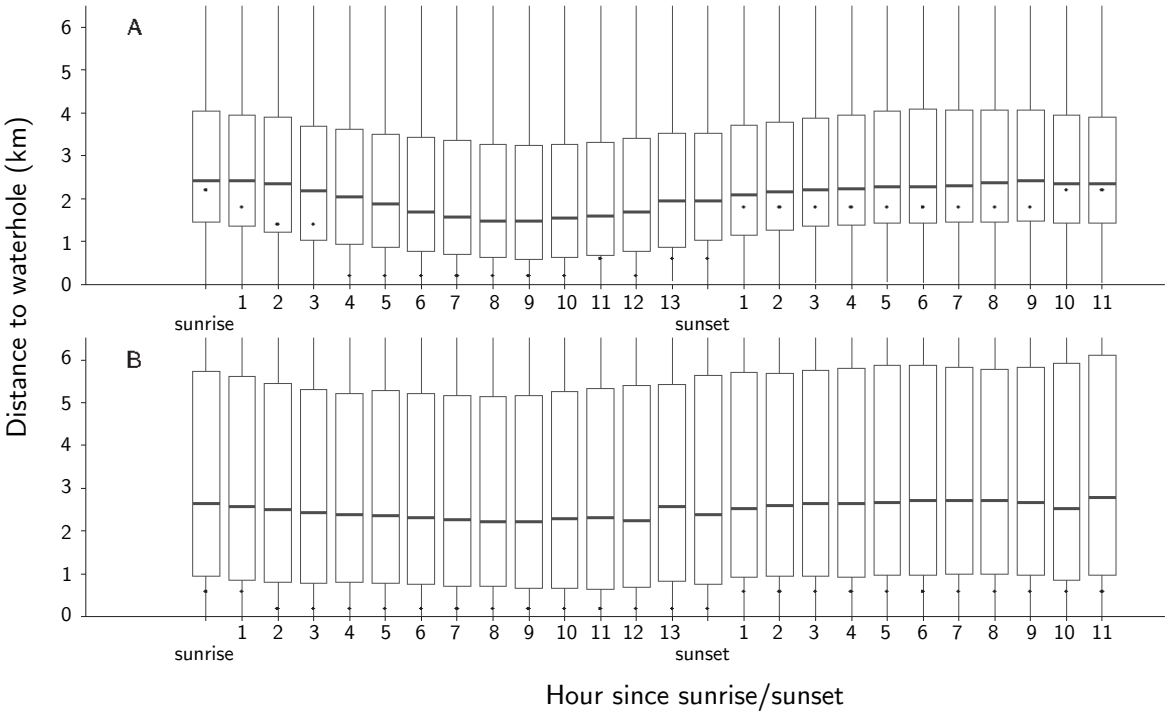
Appendix S1. Diel space use pattern of zebras

Figure S1.1 – Distribution of GPS locations of zebras as a function of the distance to waterhole for each hour elapsed since the sunrise or sunset in dry (A) and wet (B) seasons. Each boxplot shows the 25th percentile (bottom), the 75th percentile (top) and the median (dark line). As the distributions were strongly right-skewed (many short distances to waterhole, a few large ones, the y-axis is truncated at 6km), the modal value of the distribution is also shown (solid circle). We defined daytime as the period ranging from 4h to 13h after the sunrise (thus excluding the displacement phase of the early morning). Nighttime was defined as the period ranging from 1h to 11h after the sunset (thus excluding the displacement phase at sunset).



Appendix S2. Spatial predictions of the risk of encountering lions during daytime and nighttime

We estimated, for dry and wet seasons, the daytime and nighttime risk of encounter with lions for zebras based on spatial predictive maps of relative intensity of occurrence of lions. We built these maps by fitting resource selection functions (Manly et al. 2007; Johnson et al. 2013, RSF) using GPS-data collected from 46 lions, collared over the same area and the same period than zebras by qualified personnel using standard protocols (Fahlman et al. 2005). Collars acquired locations at 1h or 2h intervals during the night and every 2h or 2 or 3 times during the day. For each season and each daytime or nighttime period, we fitted a RSF model to those location data, including vegetation type, distance to waterhole and an interaction between them as predictors. Vegetation types were represented by six classes, obtained from the analysis and ground-truthing of Landsat-7 ETM+ satellite images (30-m resolution) (see Courbin et al. (2016) for details). Vegetation types were grassland, 3 types of bushlands (bushland-1, bushland-2, bushland-3) representing a decreasing gradient of openness, wooded bushland and woodland. Wooded bushland was the baseline vegetation type for all analyses.

RSFs were estimated with inhomogeneous Poisson point process (IPP) that gave the relative intensity (density of observations) of lions in the landscape (Aarts et al. 2013; Johnson et al. 2013; Warton and Aarts 2013). More precisely, IPPs quantify variations in the spatial density of GPS locations as a function of predictors and can be modelled with a weighted Poisson log-linear model using an appropriate framework (Warton and Shepherd 2010; Johnson et al. 2013, see). We first created a set of available locations, where each location was put at the centre of each grid cell over a regular grid with a 30-m resolution localised within the individual seasonal home range. Individual home ranges were estimated for each season using the 95% utilization distribution obtained from a kernel density estimation with a reference bandwidth (Worton 1989). We then estimated RSF coefficients using a Poisson log-linear mixed model, where the response value is 0 for available locations and a count number n for GPS locations. For a given GPS location i, ni is the total number of GPS locations occurring in the same cell as i plus one for the available location. All locations are given a prior weight equalled to 1/ni (Aarts et al. 2013). We added a random intercept to account for the unbalanced number of locations collected across individuals (Gillies et al. 2006). Spatial predictions of lion intensity were not affected by any residual autocorrelation because serial correlation does not bias parameters estimates (Azzalini 1994).

Table S2.1 – **Candidate lion RSF models.** Maximum log-likelihood (LL), Akaike information criteria (AIC), relative AIC values (ΔAIC) and AIC weight (w) are shown. All models had the same number of parameters (K=12) and included the vegetation type, the distance to waterhole (either raw or log-transformed values) and their interactions as predictors. The column 'Tranformation' refers to the transformation applied to the 'distance to waterhole' predictor.

Season	Period	Transformation	LL	AIC	ΔAIC	w
Dry	Daytime	none (raw values)	-167937.5	335900.9	5058.1	<0.001
		log(1+ raw values)	-165408.4	330842.8	0	>0.999
Dry	Nighttime	none (raw values)	-261526.9	523079.7	8318.5	<0.001
		log(1+ raw values)	-257367.6	514761.2	0	>0.999
Wet	Daytime	none (raw values)	-347375.4	694776.8	5227.1	<0.001
		log(1+ raw values)	-344761.8	689549.7	0	>0.999
Wet	Nighttime	none (raw values)	-477051.7	954129.4	6911.2	<0.001
		log(1+ raw values)	-473596.1	947218.2	0	>0.999

Previous works have shown that lion occurrence decreases with the distance to waterhole (Valeix et al. 2010; Courbin et al. 2016). Here, we modelled this pattern by comparing the fit of RSF models with either a raw distance to waterhole values or their log-transformed values, as predictor. Each time, the RSF model with the log-transformed values provided a much better fit on the basis of the Akaike information criterion (AIC) and Akaike weights (table S2.1). Variance inflation factor (VIF) was < 10 for all covariates of our top-ranked models, thereby allowing for valid statistical inference (Chatterjee et al. 2000). These top-ranked models were highly robust to cross validation in dry season (> 0.90) and in a lesser extent in wet season (> 0.52) (Boyce et al. 2002). We therefore used these models to describe zebra-lion encounter risk. The models showed that lion occurrence differed more between daytime and nighttime than between seasons (table S2.2, fig. S2.1). Notably, the relative risk of encountering lions decreased more rapidly as the distance from waterhole increased during nighttime that during daytime. Generally, risk of encountering lions increased in grasslands and the two most open bushlands and this was more marked during nighttime (table S2.2, fig. S2.1).

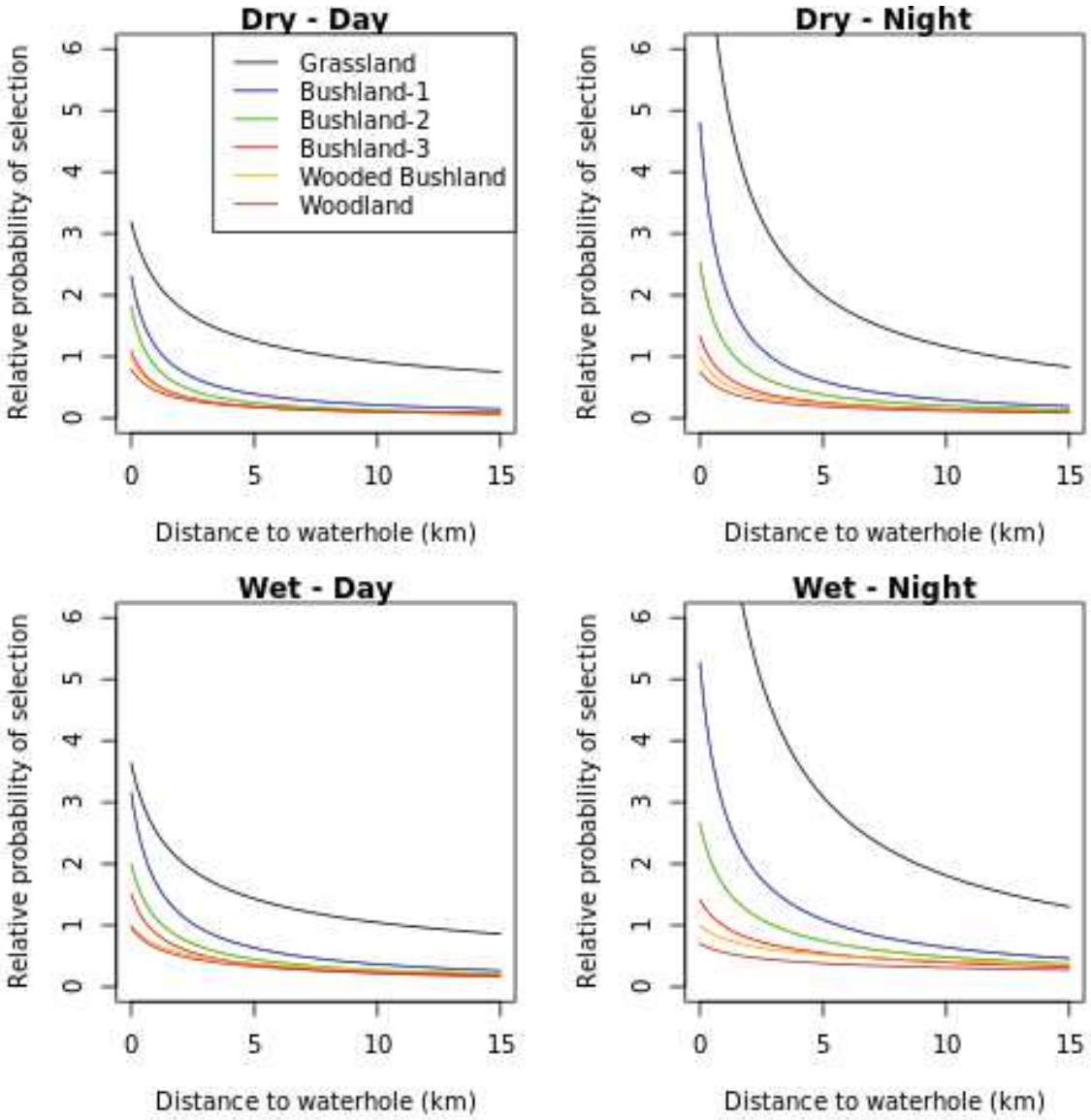
Table S2.2 – Mixed-effect models of resource selection function for lions during daytime and nighttime in the dry (n=40) and the wet (n=46) seasons. Selection coefficients (β) and their 95% confidence intervals (95% CI) are shown. Wooded bushland is the reference category for habitat type.

	Dry				Wet			
	Daytime		Nighttime		Daytime		Nighttime	
Variable	β	95% CI	β	95% CI	β	95% CI	β	95% CI
Grassland	1.16*	1.08;1.24	2.29*	2.23;2.35	1.29*	1.23;1.35	2.71*	2.67;2.75
Bushland-1	0.84*	0.76;0.92	1.57*	1.51;1.63	1.15*	1.09;1.21	1.66*	1.60;1.72
Bushland-2	0.59*	0.51;0.67	0.93*	0.87;0.99	0.69*	0.63;0.75	0.98*	0.94;1.02
Bushland-3	0.09	-0.01;0.19	0.29*	0.21;0.37	0.41*	0.35;0.47	0.35*	0.29;0.41
Woodland	-0.23	-0.47;0.01	-0.27*	-0.47;-0.07	-0.04	-0.18;0.10	-0.35*	-0.49;-0.21
Log(1+distance to waterhole (km))	-0.94*	-0.98;-0.90	-0.82*	-0.86;-0.78	-0.55*	-0.57;-0.53	-0.36*	-0.38;-0.34
Grassland x distance to waterhole	0.42*	0.36;0.48	-0.08*	-0.12;-0.04	0.03	-0.01;0.07	-0.52*	-0.56;-0.48
Bushland-1 x distance to waterhole	-0.05	-0.11;0.01	-0.34*	-0.38;-0.30	-0.35*	-0.39;-0.31	-0.52*	-0.56;-0.48
Bushland-2 x distance to waterhole	-0.17*	-0.23;-0.11	-0.24*	-0.28;-0.20	-0.29*	-0.33;-0.25	-0.35*	-0.37;-0.33
Bushland-3 x distance to waterhole	-0.04	-0.10;0.02	-0.11*	-0.17;-0.05	-0.25*	-0.29;-0.21	-0.17*	-0.21;-0.13
Woodland x distance to waterhole	0.12	-0.02;0.26	0.04	-0.08;0.16	-0.05	-0.13;0.03	0.02	-0.04;0.08

* 95% confidence intervals exclude zero.

Notes: Models were robust to cross-validation, with of 0.90 (95% CI = 0.85;0.95) for daytime and 0.95 (0.91;0.99) for nighttime models in the dry season, and of 0.52 (0.38;0.65) for daytime and of 0.87 (0.74;0.99) for nighttime models in the wet season.

Figure S2.1 – Relative risk of encountering lions in the different vegetation types as a function of distance to waterhole during daytime and nighttime, in the dry season and wet seasons.



En complément du chapitre sur les migrations quotidiennes chez le zèbre des plaines, je présente maintenant des analyses complémentaires sur des données de vigilance sur le même site d'étude, ainsi qu'un chapitre annexe de méthodologie présentant une méthode de segmentation-classification. J'ai récolté les données de vigilance lors d'une session de terrain en juillet 2015. L'idée était de regarder si l'on observait une augmentation de vigilance à l'approche du crépuscule, ce qui serait lié à l'augmentation du risque nocturne. Le jeu de données récoltées était cependant relativement limité et je n'ai donc pas poursuivi les analyses. Aussi, il était difficile de mesurer la vigilance par faible luminosité. De plus, comme on l'a vu précédemment, les zèbres s'éloignent généralement des points d'eau la nuit, et donc des milieux ouverts facilement accessibles pour des observations.

Pour contourner ces difficultés et pouvoir étudier les ajustements quotidiens des investissements anti-prédateurs lorsque le risque de prédation est fortement structuré temporellement, j'ai voulu me servir des données d'activités disponibles sur un certain nombre de colliers GPS déployés dans les années passées. Ces capteurs d'activité mesurent l'accélération sur deux axes, agrégée par intervalles de 4 minutes. Si la résolution temporelle n'est pas suffisante pour distinguer la vigilance des autres comportements, elle doit néanmoins permettre d'accéder aux modes comportementaux de l'individu : approvisionnement, repos ou déplacement. Pour distinguer ces différents modes on peut utiliser des méthodes de segmentation, qui identifient des segments homogènes en moyenne et variance au sein d'une série temporelle.

C'est dans ce but que j'ai participé à un projet pour développer une méthode de segmentation-classification bivariée, qui permet d'attribuer des classes aux différents segments estimés. L'objectif était d'utiliser la méthode de segmentation-classification pour estimer les modes comportementaux à partir des données d'activité, mais nécessitait de pouvoir valider les modes ainsi estimés à partir d'observations sur le terrain. Malheureusement, les observations précédentes n'étaient pas suffisantes (colliers non récupérés, capteurs défaillants) et la session de terrain à laquelle j'ai participé à l'été 2016, n'a pas permis de compléter ces observations (capteurs défaillants, difficultés diverses pour poser des nouveaux colliers). Cette méthode n'a donc pas pu être appliquée pour pouvoir estimer les modes comportementaux chez le zèbre des plaines et pouvoir ainsi étudier la dynamique d' approvisionnement au cours du cycle circadien. Étant donné l'investissement important dans ce projet, je présente néanmoins la méthode dans le chapitre annexe qui suit.

La vigilance augmente-t-elle à l'approche du crépuscule ?

Rémi Patin, Daniel Fortin, Simon Chamaillé-Jammes

Analyses complémentaires

Résumé

Les proies ajustent leurs comportements anti-prédateur en fonction de la dynamique temporelle du risque, notamment en fonction du jour et de la nuit, un patron temporel important de variation du risque de prédation. À Hwange on sait déjà que le zèbre des plaines (Equus quagga) effectue des migrations quotidiennes pour s'éloigner la nuit des points d'eau, où le risque de rencontre avec les lions (Panthera leo) est alors localisé. Dans cette étude on a essayé de montrer si ces ajustements spatiaux étaient complétés par des changements de vigilance à l'approche de la période risquée, au crépuscule. Pour cela on a effectué des mesures de vigilance du début d'après-midi au début de nuit. Les résultats montraient l'importance de l'habitat et du site d'étude dans les déterminants de la vigilance. Il n'y avait cependant pas d'effets de la taille du groupe ni de l'approche du crépuscule sur la vigilance.

Introduction

Le risque de prédation des proies n'est pas constant dans le temps, mais peut varier à plusieurs échelles temporelles, par exemple au cours des saisons (Jędrzejewski et al. 2002; Sperry et al. 2008; Tolon et al. 2009) ou de la journée (Valeix et al. 2009 ; Fortin et al. 2015 ; Chapitre 2). Si on observe de nombreuses adaptations morphologiques au risque de prédation, comme par exemple les capacités de course chez les ongulés (Bro-Jørgensen 2013), elles ne permettent généralement pas de s'adapter aux changements temporels de risque de prédation, ce que le comportement peut permettre de faire plus facilement (Lima and Dill 1990).

La théorie sur l'ajustement des comportements anti-prédateurs aux variations du risque, et en particulier la théorie de l'allocation du risque (Lima and Bednekoff 1999b), prévoit que les investissements anti-prédateurs à un instant ne dépendent pas que du risque actuel, mais de la distribution temporelle globale du risque. Les alternances jour/nuit constituent un des patrons de variation les plus connus du risque de prédation et peuvent contraindre fortement l'évolution des défenses anti-prédateurs (Stankowich and Caro 2009). On a de nombreux exemples empiriques d'ajustement des comportements anti-prédateurs au cycle jour/nuit (Tolon et al. 2012 ; Fortin et al. 2015 ; Padié et al. 2015 ; Chapitre 2). Les paons (*Pavo cristatus*) utilisent des stratégies anti-prédateurs différentes le jour et la nuit (Yorzinski and Platt 2012). Les perdrix (*Perdrix perdrix*) restent loin du couvert végétal la nuit (Tillmann 2009). Les chevreuils (*Capreolus capreolus*), durant la période de chasse, sont plus vigilants pendant la journée (Sönnichsen et al. 2013).

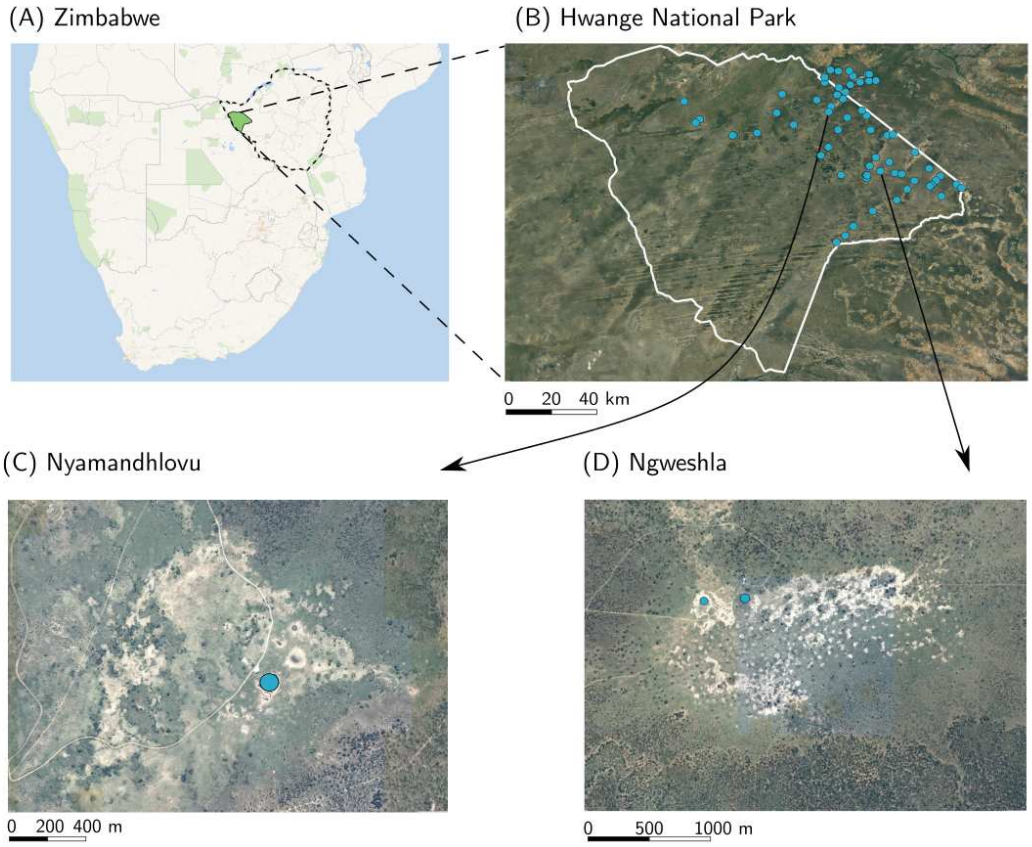
Les comportements anti-prédateurs interviennent cependant rarement de manière isolée et pour bien comprendre les compromis auxquels une proie fait face pour s'adapter à la variabilité temporelle du risque de prédation il faut pouvoir tenir compte de l'ensemble des investissements anti-prédateurs à même d'être ajustés (voir le Chapitre 1). Par exemple, dans le Chapitre 2, on a montré qu'on observe chez le zèbre des plaines (Equus quagga) un éloignement quotidien des points d'eau la nuit. Cet éloignement permet de réduire le risque de rencontre avec les lions, localisé autour des points d'eau, la nuit. Du fait de l'importance de la vigilance chez les ongulés (Liley and Creel 2008; Périquet et al. 2012; Sönnichsen et al. 2013; Creel et al. 2014), on peut s'attendre à une augmentation de la vigilance la nuit en réponse à l'augmentation du risque. Cependant l'efficacité moindre de la vigilance quand la luminosité est réduite peut diminuer son intérêt. De plus, comme les zèbres diminuent déjà leur risque de rencontre du fait de leurs migrations quotidiennes, on peut aussi s'attendre à ce que la vigilance ne change pas la nuit.

Ce chapitre d'analyses complémentaires s'appuie donc sur des observation de la vigilance chez le zèbre des plaines sur le terrain, afin de vérifier si l'on observe une augmentation de vigilance la nuit et permettre de mieux comprendre les ajustements comportementaux aux variations temporelles du risque de prédation. Il était cependant techniquement difficile de mesurer la vigilance durant la nuit, du fait de la visibilité réduite mais aussi parce que les zèbres s'éloignent généralement des points d'eau la nuit (Chapitre 2), et se retrouvent facilement isolés dans des endroits de la zone d'étude peu accessibles et difficilement repérables. Pour pallier ce problème, j'ai étudié les changements

de vigilance sur l'après-midi, en considérant que le crépuscule présente déjà un risque plus important, ce que l'on voit notamment à travers les ajustements spatiaux des zèbres (Chapitre 2).

Méthodes

FIGURE 1 – **Localisation des sites d'études.** A, le Zimbabwe. B, le parc national de Hwange. En bleu les points d'eau artificiels. C, Nyamandhlovu. D, Ngweshla.



Afin d'étudier si les zèbres sont plus vigilants à l'approche du crépuscule, j'ai réalisé des observations comportementales sur deux sites dans le Parc National de Hwange, au Zimbabwe (voir fig. 1), où la répartition de points d'eau artificiels détermine fortement celle des zones ouvertes, milieu riche en fourrage pour les paisseurs. Les deux sites retenus, Nyamandhlovu et Ngweshla ont été choisis pour leur accessibilité ainsi que la taille de leur zone ouverte, qui garantissait une chance plus forte d'observer des groupes de zèbres. Les observations ont été réalisées pendant deux semaines, en juillet 2015, pendant la saison sèche froide. Un site était visité chaque jour et les observations étaient effectuées depuis un véhicule qui circulait en boucle sur les routes autour du site en question. Lorsqu'un groupe de zèbres était rencontré, je procédais à deux types différents d'observations à l'aide d'une caméra. L'intégralité du groupe était d'abord filmé, afin d'enregistrer le comportement de chaque individu du groupe. Ensuite je faisais une ou plusieurs observations individuelles pour mesurer la longueur d'une séquence d'approvisionnement

et d'une séquence de vigilance. Un même groupe n'était pas ré-échantillonné à moins de 30 minutes d'intervalle.

Dans l'observation générale du groupe, le comportement retenu pour chaque individu était celui qu'il adoptait lors de sa première apparition dans la vidéo. Les différents comportements étaient : fourragement (un individu statique qui paît), recherche (un individu qui avance, la tête baissée), recherche en fourrageant (un individu qui avance en paissant), marche, vigilance dans l'axe (un individu qui a la tête haute et regarde devant lui), vigilance de côté (un individu qui a la tête haute et regarde sur le côté), repos (un individu debout et immobile), allongé par terre et autres (interactions sociales par exemple). Le zèbre des plaines forme des groupes sociaux relativement stables dans le temps, constitués d'un mâle et d'une ou plusieurs femelles et leurs jeunes (Fischhoff et al. 2007). On trouve aussi des groupes plus dynamiques dans le temps, constitués uniquement de mâles. Malgré cette organisation sociale assez stable, les groupes s'associent également entre eux (Fischhoff et al. 2007) et peuvent former, en particulier dans les zones ouvertes, des associations de taille conséquente (plusieurs dizaines d'individus).

Étant donné l'étendue parfois importante des groupes, il n'était pas forcément pertinent d'utiliser la taille totale du groupe, afin de contrôler pour les effets de détection et de dilution (Dehn 1990; Bednekoff and Lima 1998; Caro 2005; Lehtonen and Jaatinen 2016). Dans ce but, j'ai utilisé deux mesures : la distance au plus proche voisin et le nombre de voisins dans un cercle de taille constante. Étant donné que les données était analysées par vidéo, l'estimation de la distance au plus proche voisin est comptée en nombre de zèbres pour avoir une mesure plus fiable. Le nombre de voisins est compté dans un rayon de dix zèbres, en estimant qu'au delà, les individus sont trop éloignés pour influencer les investissements anti-prédateurs. La présence de couvert et plus généralement l'habitat pouvant influencer la vigilance (Burger et al. 2000; Creel et al. 2014; Pays et al. 2012; Périquet et al. 2012), le milieu dans lequel évoluait le groupe était aussi noté, ouvert ou fermé selon la quantité de végétation arbustive dans les alentours. L'heure de chaque observation était notée et permettait de calculer le temps jusqu'au coucher de soleil, à partir de l'heure théorique du coucher de soleil. Les différentes variables ont été groupées en catégories de taille d'échantillons similaires. Étant donné le faible nombre d'observations de comportement de vigilance, il était difficile de construire un modèle fiable qui puisse estimer les changements de vigilance en fonction du temps jusqu'au coucher de soleil en tenant compte des autres facteurs mesurés. Les résultats montrent donc seulement les données brutes c'est-à-dire la proportion d'individus vigilants en fonction du temps jusqu'au coucher de soleil, du nombre de voisins et de la distance au plus proche voisin, dans 4 situations différentes combinant les divers sites et le type de milieu, ouvert ou fermé.

Pour l'analyse des observations individuelles, je repérais un individu et commençais à enregistrer au début d'une séquence d'approvisionnement, pour pouvoir mesurer la longueur d'une séquence de vigilance et d'une séquence d'approvisionnement. J'arrêtais l'enregistrement lorsqu'une deuxième séquence de fourragement commençait après une séquence de vigilance. Si l'individu montrait une vigilance dirigée vers le véhicule, ou un signal extérieur (véhicule de touriste par exemple), j'arrêtais l'observation. Étant donné le peu de vigilance des individus, j'arrêtais l'enregistrement des séquences de fourragement

au bout de 3 minutes. Certaines observations n'ont donc pas de séquences de vigilance associées. En plus du temps de vigilance et d'approvisionnement, je notais l'heure de la journée et le milieu, ouvert ou fermé. Le nombre de voisins et la distance au plus proche voisin n'étaient pas mesurés étant donné que ces variables peuvent changer assez fortement en trois minutes. 91 observations individuelles ont été réalisées, dont 33 où l'approvisionnement durait plus de 3 minutes et dont le temps de vigilance était considéré comme nul. Les résultats montrent la proportion du temps de vigilance sur le temps total d'enregistrement en fonction du milieu, du site et du temps jusqu'au coucher de soleil. Les observations étaient trop peu nombreuses pour pouvoir construire un modèle statistique.

Résultats

Au final j'ai observé un total de 130 groupes de zèbres, soit 914 observations de comportement dont 58 de vigilance (6,3%). Les zèbres étaient plus vigilants à Ngweshla (7,9%) qu'à Nyamandhlovu (4,5%), et aussi plus vigilants dans les milieux fermés (8,3%) que dans les milieux ouverts (4%). Ces contrastes étaient les plus marquants et les plus clairs. Dans les milieux ouverts, on observait une tendance à des vigilances plus fortes autour de l'heure avant et après le coucher de soleil (fig. 2, panneaux de droite). Dans les milieux fermés, la vigilance était plus importante entre 1 et 2h avant le coucher de soleil (fig.2, panneaux de gauche). La vigilance augmentait légèrement avec la distance au plus proche voisin dans les milieux ouverts dans les deux sites et à Ngweshla dans les milieux fermés (fig. 3), même si ces patrons manquaient fortement de puissance statistique. La vigilance diminuait avec le nombre de voisins dans les milieux ouverts mais ne montrait pas de patrons clairs dans les milieux fermés (fig. 4). Les analyses individuelles de vigilance, montraient que la proportion du temps de vigilance sur le temps d'observation avait une faible tendance à augmenter à l'approche du coucher de soleil (fig. 5).

FIGURE 2 – Pourcentage d'individus vigilants en fonction du temps depuis le coucher du soleil, pour différents milieux et pour les deux sites d'étude. Le nombre d'individus échantillonnés par catégorie est affiché au-dessus des barres.

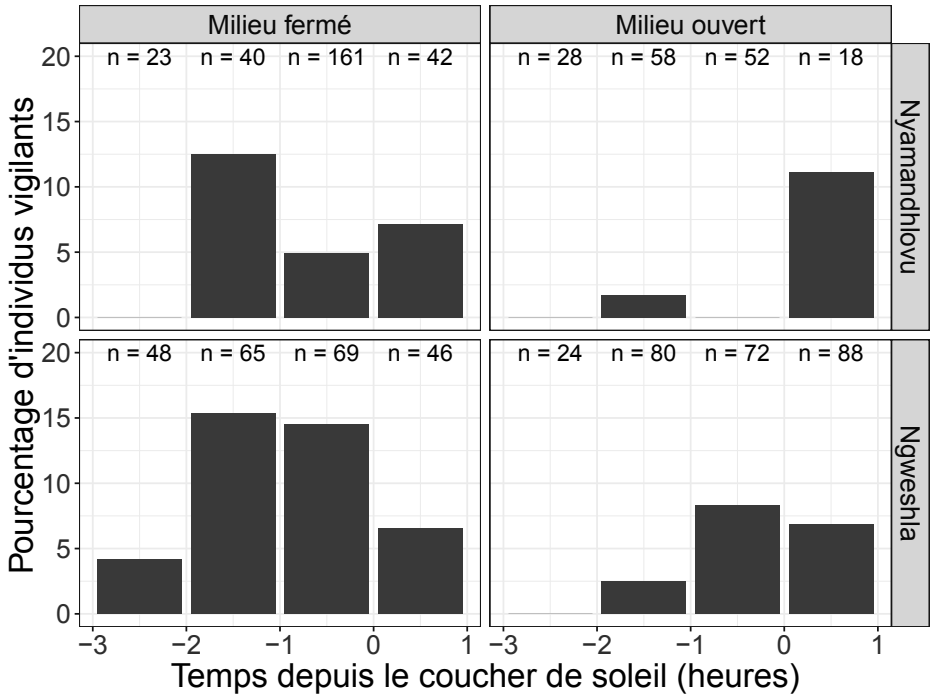


FIGURE 3 – Pourcentage d'individus vigilants en fonction de la distance au plus proche voisin, mesurée en nombre de zèbres, pour différents milieux et pour les deux sites d'étude. Le nombre d'individus échantillonnés par catégorie est affiché au-dessus des barres.

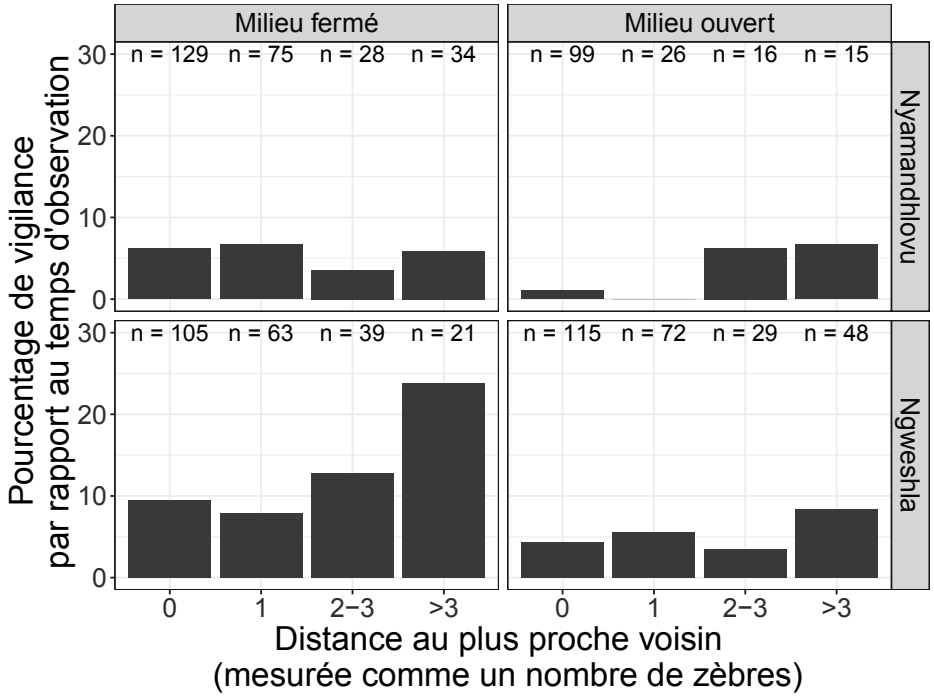


FIGURE 4 – Pourcentage d'individus vigilants en fonction du nombre de voisins dans un rayon de dix zèbres, pour différents milieux et pour les deux sites d'étude. Le nombre d'individus échantillonnés par catégorie est affiché au-dessus des barres.

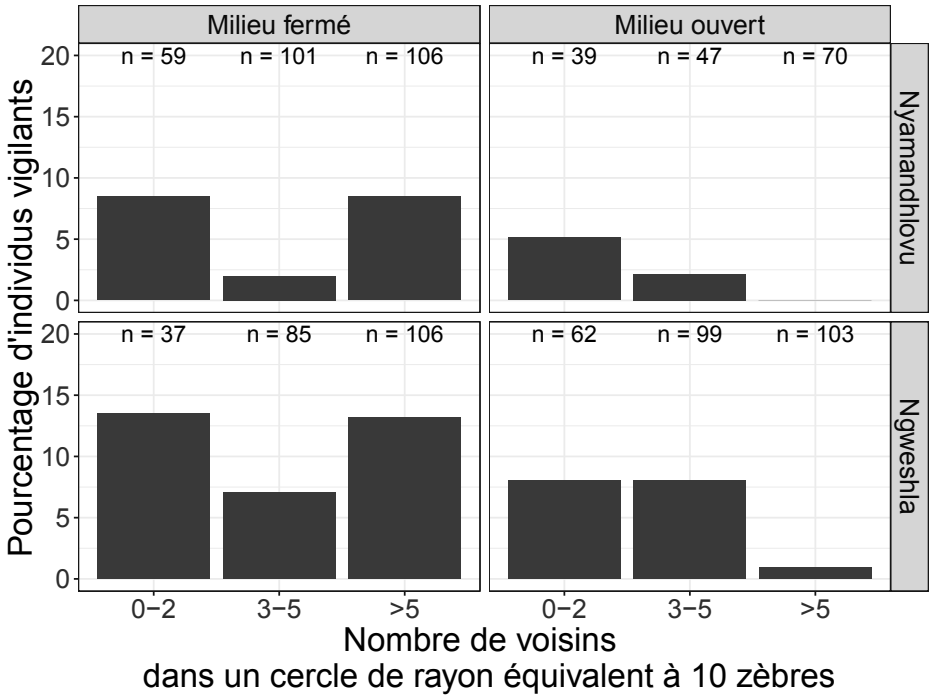
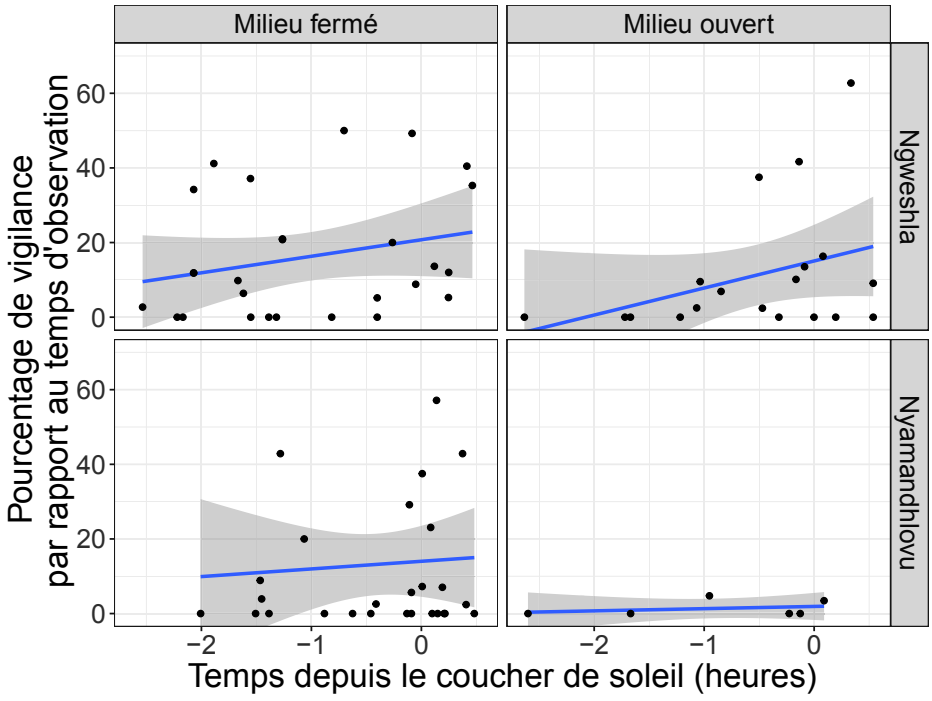


FIGURE 5 – Durée relative des comportement de vigilance dans les observations focales, pour différents milieux et pour les deux sites d'études. Une simple régression linéaire est affichée pour chaque combinaison de facteurs.



Discussion

Les résultats suggèrent une augmentation de la vigilance dans les milieux fermés ainsi que des différences entre les deux sites d'études. Les effets de l'heure de la journée ainsi que du nombre de voisins ou de la distance au plus proche voisin étaient moins clairs. La différence entre milieu fermé et milieu ouvert semble être relativement robuste à travers les différentes interactions (sites, heures de la journée, distance aux voisins, nombre de voisins) et suggère une augmentation de la vulnérabilité dans les milieux fermés, à proximité du couvert. Le couvert peut aussi profiter aux proies en tant qu'obstruction potentielle d'une attaque (Mysterud and Østbye 1999) mais cet effet n'est visiblement pas dominant ici. Bien que j'ai aussi mesuré la distance au couvert directement, nous n'avons pas montré ici cet effet direct étant donné que les distances au couvert étaient fortement liée à l'habitat. Les distance au couvert étaient en effet beaucoup plus faibles dans les milieux fermé. La vigilance était globalement plus faible à Nyamandhlovu et ce dans la plupart des situations possibles (milieu, heure de la journée, distance au voisins le plus proche et nombre de voisins). Cette différence peut provenir d'une différence globale de risque entre les deux sites, avec un risque potentiellement plus fort à Ngweshla. Le reste des effets n'était pas suffisamment clair ni avec un échantillonnage suffisant pour pouvoir les considérer robustes.

Identifying stationary phases corresponding to different movement modes or home range settlements

Identification de segments stationnaires correspondant à différents modes comportementaux ou à des domaines vitaux

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Chapitre annexe

Article en préparation

Abstract

The dynamics of processes is usually reflected in the time-series of some characteristic variables, which are often piecewise stationary. Thus identifying stationary phases is a critical first step to understand the underlying process. In movement ecology, key questions rest on identifying stationary phases corresponding to different behavioural modes such as transit, feeding and resting, or, at larger scale, to temporary home ranges. To identify these phases, we introduce a new segmentation-clustering model, segclust2d, which applies to bivariate time-series and can be easily parameterised. Using computer simulations, we show that segcust2d can outperform previous, more complex methods which were specifically developed to highlight changes in movement modes or home range shifts (based on Hidden Markov or Ornstein-Uhlenbeck modelling, respectively). Moreover, as segclust2d applies to time-series of any nature and can be generalised to any number of dimensions, it should also provide a useful analysis tool in numerous fields beyond movement ecology.

Contents

1 Introduction

Landscapes are spatially and temporally variable at various scales (Levin 1992). Animals are therefore expected to adjust their movements to the characteristics of their local environment, so as to maximize the time spent in profitable (or safe) habitats and minimize time in adverse ones (Pyke 1978). Consequently, time-series of locations or of some movement metrics (e.g. turning angle, speed) are expected to be piecewise stationary, i.e. to present a fixed mean and variance for limited periods corresponding to stationary phases, alternating with rapid transition phases corresponding to changes of area or behaviour. In movement ecology, depending on the metrics considered, stationary phases result from the exploitation of a given area (locational stationarity) or the display of a given behaviour (behavioural stationarity). Identifying these phases is a prerequisite to determine the biologically relevant scales of movement (Benhamou 2014). It is therefore of paramount importance in two types of movement studies:

Identifying behavioural modes. Foragers are generally expected to alternate intensive (area-concentrated) searching phases, characterized by high tortuosity and low speed, and extensive searching (transit) phases, characterized by low tortuosity and high speed (Dias et al. 2009). Although different segmentation approaches were developed to identify behavioural modes by looking at breakpoints (i.e. rapid transitions between stationary phases Barraquand and Benhamou 2008; Gurarie et al. 2009; Nams 2014), a more sophisticated approach based on State Space / Hidden Markov Models (Patterson et al. 2008, HMM) have gain momentum in recent years. By focusing on the joint time-series of step lengths and turning angles calculated from successive relocations, this approach attempts to attribute any relocation to a predetermined number of behavioural modes modelled as hidden states. This approach however can be cumbersome to implement. In particular, the suitable convergence of the HMM-based segmentation-clustering process requires specifying informative priors, which can be a tricky task.

Identifying home range shifts. This recently emerging question has been addressed in terms of movement scales (Benhamou 2014) and of migration characteristics (Naidoo et al. 2012; Cagnacci et al. 2016). For a migratory animal, the time-series of relocations coordinates can be assumed to be stationary for some time, when the animal exploited the area where it established its temporary (e.g. seasonal) home range, then to be non-stationary for a relatively short time, corresponding to the migration period, and to be again stationary for some time as soon as the animal established a new home range, and so on. It is worth noting that a shift in home range does not necessarily involve a shift in mean location. It may also correspond to a change in variance if the animal enlarged or shrank its home range, e.g. due to a change in season (Naidoo et al. 2012; Monsarrat et al. 2013) or in reproductive status. Various methods were proposed to detect home range shifts. The simple univariate approach based on the evolution of the beeline distance from the starting point (Bunnefeld et al. 2011) sounds interesting but fully misses

movements leading the animal at a similar distance from the starting point but in another direction. A more complex approach rests on multiple-state Ornstein-Uhlenbeck modelling (OUM Breed et al. 2017; Gurarie et al. 2017). However, as it involves that all home range phases and shifts are explicitly modelled, this approach tends to become cumbersome when there are more than a single shift.

Here we introduce a new model able to segment a bivariate time-series, and to cluster similar segments (corresponding to stationary phases) in a common class (corresponding to a given state) if desired. We demonstrate that this model, which is easy to use and parameterise, can successfully identify stationary phases corresponding to temporary home ranges when based on bivariate locational time-series, as well as movement modes when based on bivariate time-series of metrics such as speed and tortuosity. It thus offers an efficient and user-friendly alternative to previous, more complex, approaches. Furthermore, as this model applies to bivariate piecewise stationary time-series based on any kind of metrics and can be straightforwardly extended to deal with multi-variate series, it can potentially be used not only in movement ecology but in many other fields by focusing on appropriate metrics.

2 Methods

2.1 Statistical model

General principle. Consider a piecewise bivariate stationary signal provided by two time-series composed of an unknown number of stationary phases common to the two series. Both series are assumed to be regular (no gaps), and may need to be normalized if they are of different nature, so as to have the same weight in subsequent procedures. One needs a reliable statistical model to find and characterize these phases, and possibly to cluster them when they are assumed to be the expressions of a limited number of unobserved states of the underlying process (e.g. behavioural modes). The segmentation process raises two main issues from a statistical and algorithmic point of view when attempting to maximize the likelihood of the result: (i) determining the optimal number of segments and (ii) for a given number of segments, finding the optimal segmentation, i.e. determining the locations of the starting/ending points of the segments (breakpoints). The latter reduces to a well-known discrete optimization problem solved using a dynamic programming algorithm introduced by Bellman (1954; for a recent example, see Rigaill 2015). With n sites where the signal can be cut and K segments, the dynamic programming algorithm reaches the exact maximum likelihood solution with a complexity in $O(n^2K)$, far smaller than the complexity in $O(n^K)$ involved by a force brute algorithm exploring the whole segmentation space. We will first introduce the models to optimally segment a bivariate signal for a predefined number of segments K and possibly (if clustering is required) a predefined number of states M. Afterwards, we will show how the optimal number of segments and possibly of clusters can be found based on penalized likelihood. Our approach is based on Lavielle (2005)'s segmentation method of univariate

signals and its extension by Picard et al. (2007) to segment and cluster DNA sequences without assuming any kind of distribution for the segment lengths, such as a geometric distribution as HMM implicitly do.

Optimal segmentation in K **segments, with optional clustering in** M **states.** Assume that there are K stationary phases in a bivariate time-series with total length n. A stationary phase corresponds to a segment. It is defined by a sequence of consecutive random variables sharing the exact same distribution, in particular the same mean $\boldsymbol{\mu}$ and variance matrix $\boldsymbol{\sigma}^2$. As soon as one of these parameters changes, a new segment starts. Both components within a given segment $k \in [1,...,\mathrm{K}]$ starting at time $t = t_{k-1}+1$ and ending at time $t = t_k$ (with $t_0 = 0$ and $t_\mathrm{K} = n$) are modelled as sequences of Gaussian independent random variables $b\mathrm{Y}_t$. In the absence of clustering (segmentation-only model), the value of the bivariate signal (with two components labelled 1 and 2) at time t is modelled simply as follows:

$$\mathbf{Y}_t \sim \mathscr{N}(\boldsymbol{\mu}_k, \boldsymbol{\sigma}_k^2) \text{ with } \boldsymbol{\mu}_k = \begin{pmatrix} \mu_{k,1} \\ \mu_{k,2} \end{pmatrix} \text{ and } \boldsymbol{\sigma}_k^2 = \begin{pmatrix} \sigma_{k,1}^2 & 0 \\ 0 & \sigma_{k,2}^2 \end{pmatrix} \tag{2.1}$$

where $\boldsymbol{\mu}_k$ and $\boldsymbol{\sigma}_k^2$ are the mean and variance matrix of the bivariate Gaussian distribution $\mathscr{N}(\boldsymbol{\mu}_k, \boldsymbol{\sigma}_k^2$ for segment k. As the model parameters to be estimated vary independently between segments, dynamic programming can be used to segment the bivariate signal at best in K segments. Its application is straightforward in this case, as it relies on the log-likelihood of each segment, which is simply equal to the sum of the log-likelihoods of the two components.

In the segmentation-clustering model, a state m, among M possible states, is assigned to every segment, and random variables within a segment classified in state m are all assumed to share the same mean $\boldsymbol{\mu}_m$ and variance $\boldsymbol{\sigma}_m^2$, different from those involved in other states. More formally, let (S_k), with $k = 1,...,\mathrm{K}$, denote the state of the segment k: S_k is a latent random variable taking values in $[1,...,\mathrm{M}]$. It is modelled through a multinomial distribution of parameters $\pi = (\pi_m)$ with $m = 1,\ldots,\mathrm{M}$, where π_m corresponds to the probability for a segment to belong to state m. Given $\mathrm{S}_k = m$, the value of the bivariate signal at time t, $\mathbf{Y}_t$, is therefore modelled as:

$$\mathbf{Y}_t|\mathrm{S}_k = m \sim \mathscr{N}(\boldsymbol{\mu}_m, \boldsymbol{\Sigma}_m) \text{ with } \boldsymbol{\mu}_m = \begin{pmatrix} \mu_{m,1} \\ \mu_{m,2} \end{pmatrix} \text{ and } \boldsymbol{\sigma}_m^2 = \begin{pmatrix} \sigma_{m,1}^2 & 0 \\ 0 & \sigma_{m,2}^2 \end{pmatrix} \tag{2.2}$$

where $\boldsymbol{\mu}_m$ and $\boldsymbol{\sigma}_m^2$ are the mean and variance matrix of the bivariate Gaussian distribution $\mathscr{N}(\boldsymbol{\mu}_m, \boldsymbol{\sigma}_m^2$ for any segment k belonging to state m. As parameters $(\pi_m, \boldsymbol{\mu}_m, \boldsymbol{\sigma}_m^2)$ that characterise any state m are unknown and are to be estimated, resulting in a mixture distribution where segments are linked in terms of parameters, the optimal segmentation cannot anymore be obtained using dynamic programming alone. Following Picard et al. (2007), we designed the following two-step procedure, which is iterated up to convergence.

1. Given a set of parameters $(\pi_m, \boldsymbol{\mu}_m, \boldsymbol{\sigma}_m^2)$ with $m = 1,...,\mathrm{M}$, the best segmentation in K segments is obtained using dynamic programming.
2. Given this segmentation, the values of parameters are estimated using an

expectation-maximization algorithm which is commonly used in latent variable modelling (Dempster et al. 1977).

By mixing dynamic programming and expectation-maximization through this iterative procedure, segmentation and clustering processes work jointly (rather than the latter after the former) leading to the optimal segmentation given K and M. However, finding the optimal segmentation for a given number of states M requires an additional smoothing procedure to solve possible convergence issues (see details in Appendix 1).

Finding the optimal numbers of segments and states. For both methods (segmentation-only and segmentation-clustering), a minimum segment length L_{min} has to be set not only to speed up the algorithm, but also, more fundamentally, to prevent over-segmenting, based on biological considerations. For example, setting L_{min} to a value of a few weeks when analysing locational time-series will prevent the algorithm from considering an area exploited only for a few days, corresponding to foray outside the usual home range or to stop-over during migration, as a distinct home range. Similarly, setting L_{min} to a value of several minutes when looking for changes in behavioural modes will prevent force the algorithm to assign a given movement bout to a given behavioural mode only if this bout is long enough, even though it may be punctuated by ephemeral events related to another behaviour. To obtain the optimal solution, we calculated the likelihood of all number of segments $K < K_{max} = \lfloor \frac{n}{L_{min}} \rfloor$, and for any number of states M (< K) one wishes to consider if clustering has to be involved. In this case, the optimal values of K and M are determined as those that maximize a Bayesian Information Criterion (BIC)-based penalised likelihood taking both M and K into account (see details in Appendix 1). However, as shown in the Results section, it is usually preferable to consider a single value of M based on biologically relevant grounds than to let the model determine an optimal number of states based on a statistical basis. When only segmentation is involved (no clustering), the optimal number of segments K is based in agreement with Lavielle (2005) on maximizing a K-penalized likelihood curve (Appendix 1). Both methods have been implemented in a user-friendly R package (https://cran.r-project.org/package=segclust2d), which optionally allows K_{max} to be set to a value lower than $\lfloor \frac{n}{L_{min}} \rfloor$ for preventing the algorithm from wasting time in looking for unlikely solutions.

2.2 Computer simulations

We run simulations to assess the ability of our approach to detect home range shifts and changes in behavioural modes, and to compare it with that of other (OUM-based and HMM-based) methods. For each set of parameters of each type of simulation, we simulated 100 replicates. Distances are expressed in arbitrary unit length u.

Home range shifts. For simplicity, the animal was assumed to move with a constant speed and to behave as a central place forager. We simulated its movement as a biased

correlated random walk. At each time step, a turning angle α_i is drawn from a wrapped Gaussian distribution with a null mean and standard deviation $\sigma_i = \sigma_0 \left[1 + \frac{D_i - D_{i-1}}{2}\right]$ where D_i is the current distance to the central place, and progresses by 1 unit length ($1u$) in this new direction. This results in utilization distribution that decreases exponentially with the distance to the central place (Benhamou 1989). In a batch of simulations, σ_0 was set to 0.5 radians, and the central place was first set at a given location for the first 10,000 time steps (phase 1), then shifted to another location by $60u$ in both X and Y for 10,000 additional time steps (phase 2), resulting in disjoint home ranges, and then shifted to a third location by $20u$ in both X and Y for 10,000 additional time steps (phase 3), resulting in overlapping home ranges. In another batch of simulations, the central place remained at the same location for 30,000 time steps, but σ_0 was set to 0.7 radians for time steps 10,001 to 20,000 (phase 2) and to 0.5 radians otherwise (phases 1 and 3), involving a transitory enlargement of the home range. As fine-scale movements are uninformative (and usually ignored in field studies) in this context, we sub-sampled the data sets by keeping one location every 60.

Changes in behavioural modes. We simulated a random search movement as a correlated random walk where three types of activity – immobility (resting, standing or static foraging), intensive (area-concentrated) searching and extensive searching (transit) – alternate, each one lasting 20 time steps, this 60-step sub-series being repeated 5 times. The step lengths L_i were draw from a log-normal distribution with a mean equal to $0.5u$ in the intensive mode or $1.0u$ in the extensive mode, and with a standard deviation equal to 1/10th of the mean in both modes. Turning angles α_i were drawn from a wrapped Gaussian distribution with a null mean and a standard deviation equal to 0.4 radians in the intensive mode or 0.3 radians in the extensive mode. To mimic possible factors (e.g. GPS recording noise) that can blur the differences between modes, the locations obtained in this way, as well those obtained for immobility phases, were submitted to bivariate Gaussian random noise with a null mean and a standard deviation ζ in the range 0.25 - $0.35u$.

2.3 Metrics

For identifying home range shifts, the two variables considered are orthonormal Cartesian coordinates (x_i, y_i) of locations. When dealing with GPS data expressed in decimal degrees (longitude and latitude), such coordinates are obtained as easting and northing through a classical projection (e.g. UTM). For identifying behavioural modes, the metrics usually considered in HMM-based approaches are step lengths L_i and turning angles α_i computed from locations recorded at constant time intervals Δt, and therefore acting as proxies for linear $\left(\frac{L_i}{\Delta t}\right)$ and angular $\left(\frac{\alpha_i}{\Delta t}\right)$ speeds, respectively. We used such metrics for comparative purpose, but we also tested some variants, assumed to improve the contrast between the different modes. We computed the linear speed as $\frac{L_i + L_{i+1}}{2\Delta t}$. Although this basic smoothing introduces some serial correlation which is not taken into account in our model, it should result in a less noisy signal. Furthermore, angular speed

may show little changes between searching modes because the intensive mode usually involves both a decrease in linear speed and an increase in path tortuosity but angular speed mechanically increases with both of them (Benhamou and Bovet 1989; Barraquand and Benhamou 2008). We therefore computed turning angles α_i^* based on a constant step length r rather than at constant time interval. For this purpose, each location $\mathbf{X}_i = (X_i, Y_i)$ is considered the centre of a virtual circle with radius r, and the entrance and exit locations P_{en} and P_{ex} are determined through linear interpolation (Appendix 2). The turning angle α_i^* is then computed in $[-\pi, \pi]$ as the angular deviation between vectors $P_{en} \rightarrow X_i$ and $X_i \rightarrow P_{ex}$ (both with length r) rather than vectors $X_{i-1} \rightarrow X_i$ (with length L_i) and $X_i \rightarrow X_{i+1}$ (with length L_{i+1}) as done to compute α_i. When both L_i and L_{i+1} are larger than r, one gets $\alpha_i^* = \alpha_i$, whereas α_i^* tends, on average, to be larger (random search paths) or smaller (directed paths) than α_i when r is larger. We set r to the median of the step length distribution. In our simulations, we noticed that using a larger radius tends to improve the discrimination between the fast and slow movement modes but to worsen the discrimination between the slow movement mode and the immobility mode. We also tested the two orthogonal signals provided by the 'persistence speed' $\frac{L_{i+1}\cos(\alpha_i)}{\Delta t}$ and 'turning speed' $\frac{L_{i+1}\sin(\alpha_i)}{\Delta t}$ (Gurarie et al. 2009).

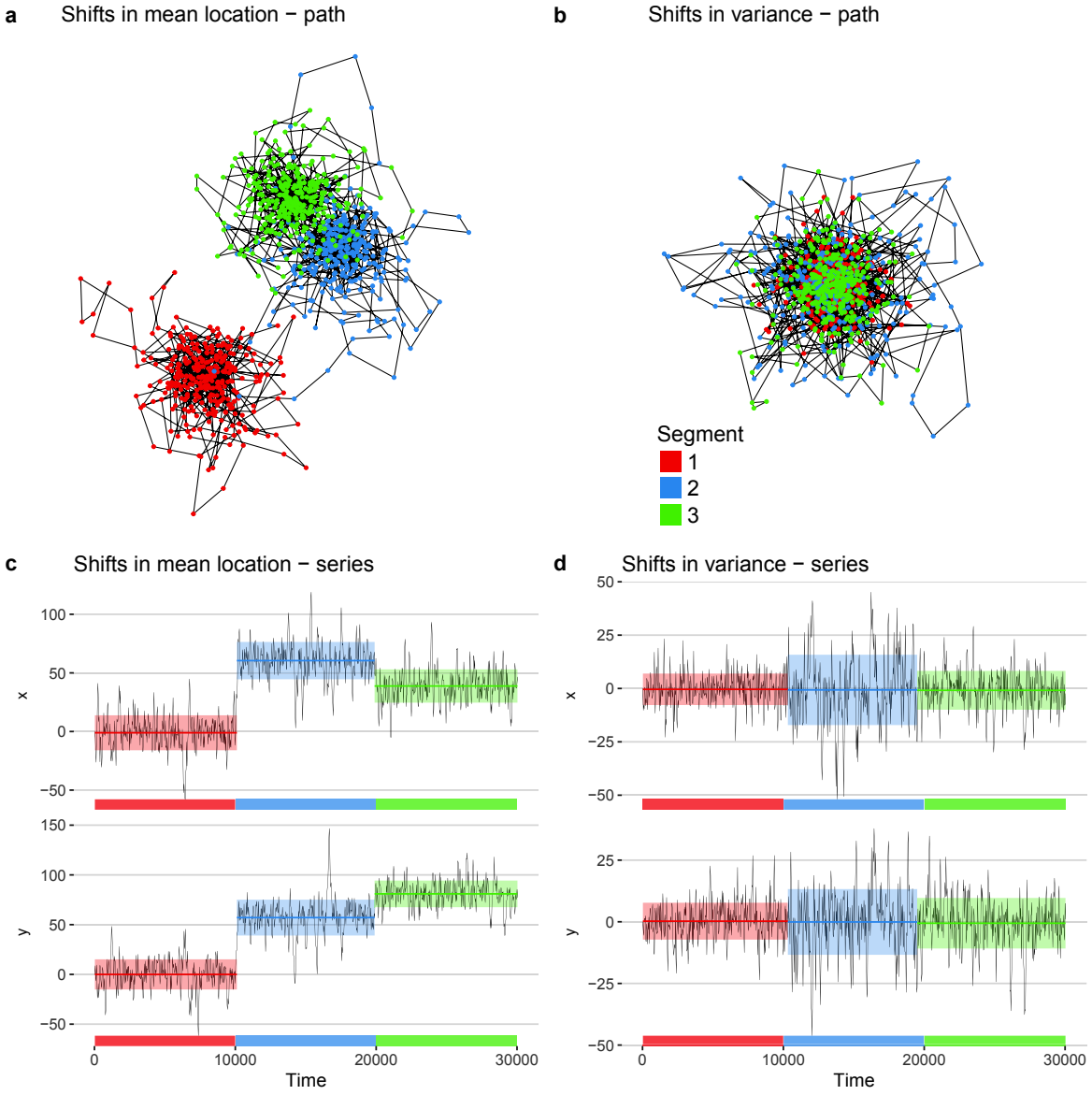
3 Results

3.1 Identifying home range shifts

Simulated movements. Figure 1 shows an example where the central place of the home range was shifted by $60u$ between phases 1 and 2, and by $20u$ between phases 2 and 3, in both X and Y, and an another example where the home range was enlarged during the phase 2 with respect to phases 1 and 3. Segclust2d/segmentation-only (with L_{min} set to 45 locations, corresponding to 2700 time steps because of the 1/60 subsampling) was able to correctly determine the true number of phases in 98 out of the 100 replicates involving shifts in mean location (i.e. central place), and 88 out of the 100 replicates involving shifts in variance (i.e. change in home range size). Furthermore, when the true number of phases has been specified, our approach appeared able to correctly estimate the occurrences of various shifts (fig. 2). In contrast, the OUM-based algorithm 'quickfit' (in 'marcher' R package) which was specifically developed by Gurarie et al. (2017) to identify home range shifts in mean location without need to specify any prior, appeared able to correctly detect such shifts only when they are large enough to result in non-overlapping home ranges (fig. 2).

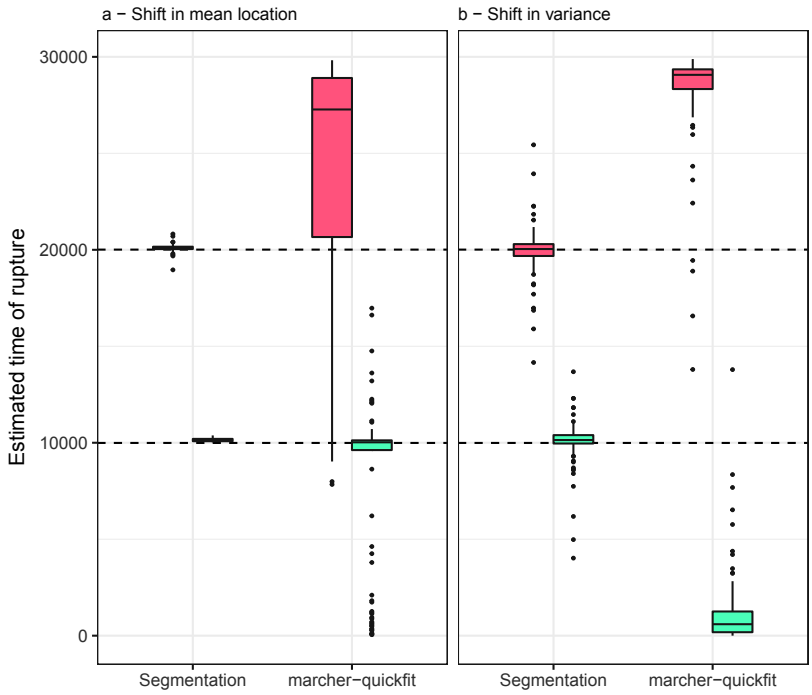
Illustrative example. We used the GPS track of an African Elephant (*Loxodonta africana*), recorded for > 2.5 years to illustrate the way segclust2d/segmentation-only can identify home ranging phases and shifts (fig. 3). Considering that a time-series is (roughly) stationary when the partial means and variances obtained for its first and second halves

Figure 1 – **Examples of segmentation-only of simulated movements using segclust2d to highlight home range phases and shifts.** Top panels show the simulated paths (after 1/60 subsampling) corresponding to three home range phases (two shifts), either in mean location (a) or in variance (b). The corresponding time series for both location coordinates (x, y) are presented in panel (c) and (d), respectively. The horizontal colour bars running along the time axis show the true occurrences of the three phases, whereas the coloured bands appearing over the x and y signals show their occurrences as estimated using the segclust2d/segmentation-only method (with Lmin = 45 locations, i.e. 2700 unit times) and provide the estimated mean (plain horizontal line running in the middle of the band) ± standard deviation (band width) for each segment separately.



or for its three thirds are not markedly different, the whole time-series of easting and northing coordinates can be said to be both stationary, corresponding to a multiannual (possibly lifetime) home range, and piecewise stationary. It can therefore be segmented to highlight temporary home ranges at smaller scale and shifts between them. However, some of the phases so highlighted are clearly nonstationary. In particular, segments 1 and 5 correspond mainly to a slow south-westwards migration (rather than a temporary home

Figure 2 – **Comparative performances of segclust2d/segmentation-only vs. an OUM-based method for highlighting home range phases and shifts.** The boxplots show the distribution of the estimated occurrences of home range shifts in mean location (left) and in variance (right), estimated from 100 replicates simulated with the same parameters as the one illustrated in fig. 1, using either segclust2d/segmentation-only with Lmin = 45 (2700 unit times) or OUM-based algorithm 'quickfit' (in 'marcher' R package; Gurarie et al. 2017). The true occurrences of the shifts are indicated by horizontal dashed lines (10000 and 20000 unit times). For both methods, the true number of segments was specified to get a fair comparison (specifying the number of segment is required by the quickfit algorithm, whereas our method proved able to find it for most replicates).

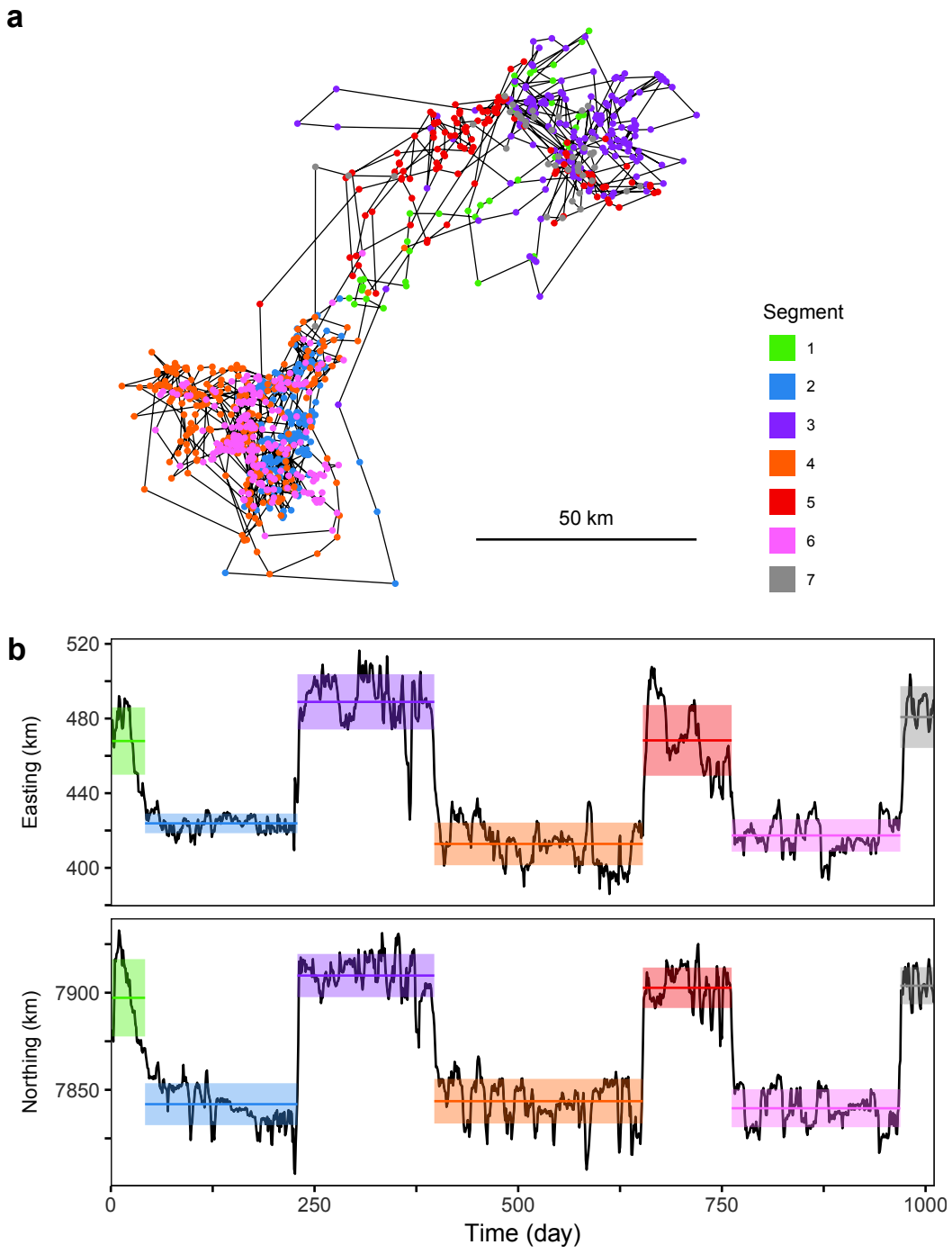


range) between the two core areas of the multiannual home range. Segment 2 also corresponds to a nonstationary, migratory (southwards moving) phase, which went through an area used as a temporary home range during segments 4 and 6. This highlights that a same area can be used in different ways at different periods.

3.2 Identifying behavioural modes

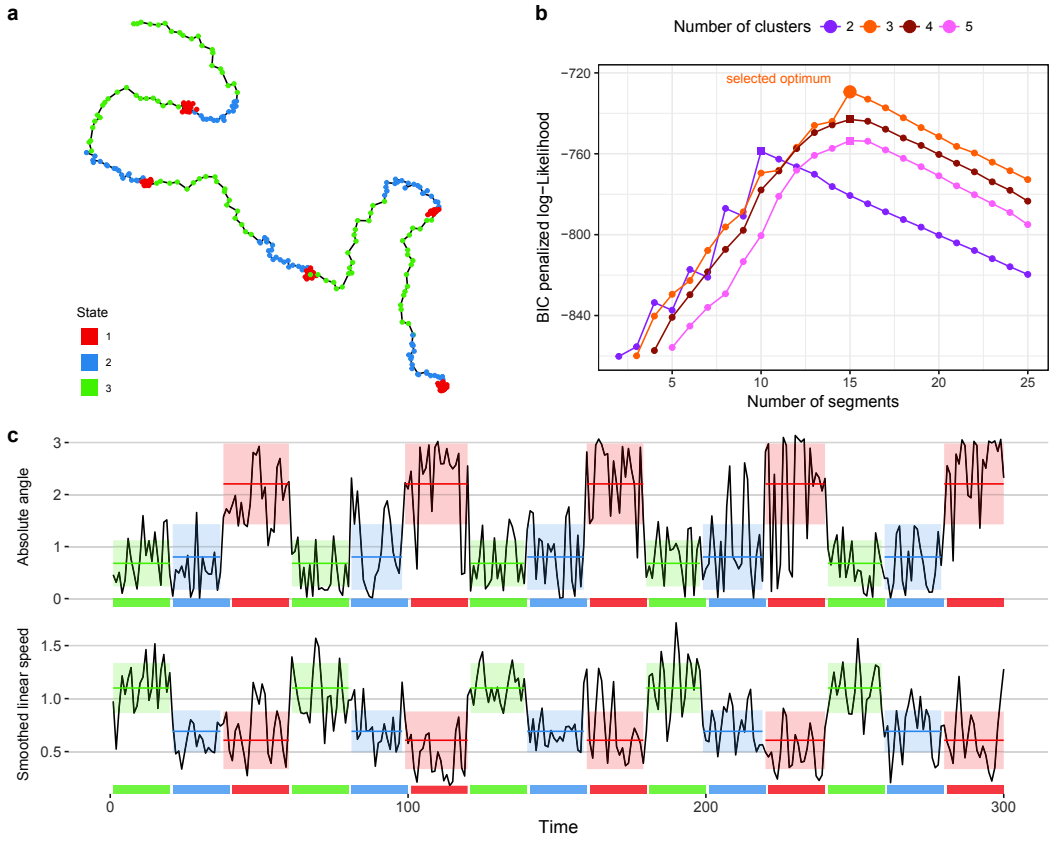
Simulated movements. An example of path with three behavioural modes (extensive searching, intensive searching and resting) is shown in fig. 4 with the corresponding time-series in terms of turning angle α_i^* and smoothed speed $\frac{L_i + L_{i+1}}{2\Delta t}$. In this example, segclust2d/segmentation-clustering appears able to detect the true number of modes (M = 3) and to attribute almost all locations to the right mode. We compared our method with a HMM-based method specifically designed to deal with movement data (Michelot et al. 2016; McClintock and Michelot 2018) when the true number of modes has been specified. The results obtained from 100 replicates showed that segclust2d/segmentation-clustering rivals with - and can even outperform - the HMM-based method although the latter was helped by very informative priors (fig. 5; see Ap-

Figure 3 – **Example of segmentation-only of an African elephant's movement recorded over 1000 days using segclust2d to highlight home range phases and shifts.** (a) Rough path representation obtained by linking the locations subsampled so as to keep a single GPS location per day; (b) Corresponding time series of locations coordinates (easting and northing). The coloured bands appearing over the time series show the estimated mean (plain horizontal line running in the middle of the band) ± standard deviation (band width) of each of the seven segments obtained using the segmentation-only method with Lmin = 30 days.



pendix 3, fig. S3.1 for results with other noise levels). It also appeared that, as expected,

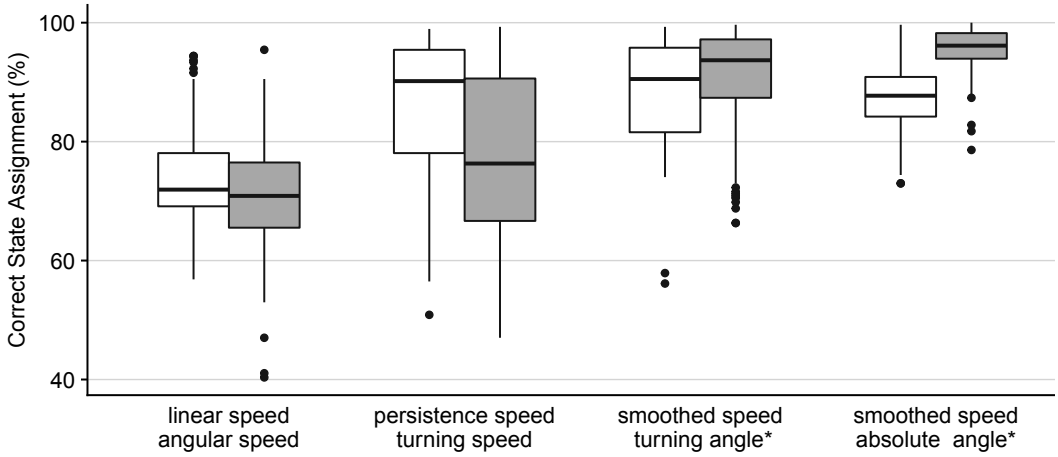
Figure 4 – **Example of segmentation-clustering of a simulated movement using segclust2d to highlight behavioural changes.** (a) Simulated path as a composite correlated random walk, with additional noise ζ = 0.3 u; (b) Determination using BIC-based penalised likelihood of the most likely numbers of states (M = 3) and segments (K = 15) (big orange dot), and of the most likely number of segments for the other three numbers of states considered (large squares at the top of the curves). (c) Corresponding time-series in terms of absolute turning angle computed with a constant step length, $|\alpha_i^*|$, and smoothed speed, $\frac{L_i + L_{i+1}}{2\Delta t}$, segmented with L_{min} = 10 and M = 3; the coloured bands appearing over the two time-series show the est +/- standard deviation (band width) for each of the three movement modes whereas the horizontal colour bars running along the time axis show the true occurrences of these modes.



the angular $\left(\frac{\alpha_i}{\Delta t}\right)$ and linear $\left(\frac{L_i}{\Delta t}\right)$ speeds are not the most suitable the metrics for detecting behavioural changes. Thus, better results were obtained with both methods when using any other of the couples of metrics considered. The best fit was obtained with absolute turning angle $|\alpha_i^*|$ and smoothed speed. With such metrics, depending on the noise level, our method can on average attribute 91-97% (vs. 84-91% for HMM) of locations to the right mode when the true number of modes is known. Otherwise, our method can estimate this number as the most likely number of clusters, but the fraction of correct estimate is too low to consider the result as reliable (Appendix 3, fig. S3.2).

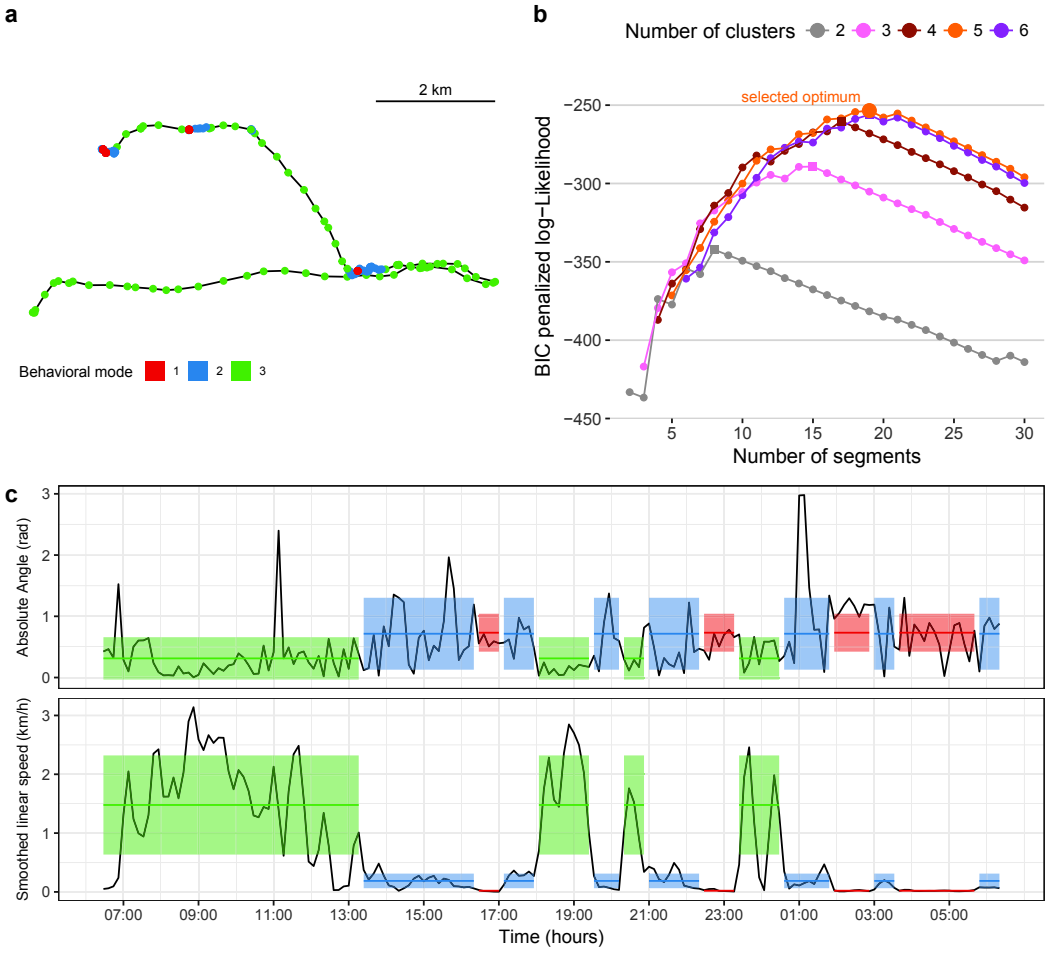
Illustrative example. We used a 24-h GPS track of a plains zebra (*Equus quagga*) to illustrate the way segclust2d/segmentation-clustering can identify the occurrences of the various movement modes (fig. 6). Although that, in this example, the most likely number

Figure 5 – **Comparative performances of segclust2d/segmentation-clustering vs. a HMM-based method for highlighting behavioural changes.** The boxplots show the proportion of correct state assignments, obtained for various bivariate signals when the true number of states is known (M = 3), as estimated from 100 replicates simulated with the same parameters as to the one illustrated in fig. 4 (noise $\zeta = 0.3$). The star (*) indicates turning angles computed with a constant step length, in terms of arithmetic (α_i^*) or absolute ($|\alpha_i^*|$) values. The white boxplots show the results obtained with HMM-based R package momentuHMM (McClintock and Michelot 2018), with Gaussian priors set to the true means and variances of the various metrics in the different states. The grey boxplots shows the results obtained using segclust2d/segmentation-clustering with $L_min = 10$.



of modes was estimated to be five, we present the segmentation obtained when setting this number to three, assuming that the biologically relevant modes should be resting (or any other non-moving behaviour such as standing), feeding and transiting (the other two modes detected by the algorithm when using 5 modes being assumed to correspond to mixed behaviours).

Figure 6 – **Example of segmentation-clustering of a 24-h zebra's movement using segclust2d to highlight behavioural changes.** (a) Path representation obtained by linking GPS locations recorded every 8 minutes; (b) Determination using BIC-based penalised likelihood of the most likely numbers of states (M = 5) and segments (K = 20) (big orange dot), and most likely numbers of segments for the other number of states considered (large squares at the top of the curves), with Lmin = 5 (i.e. 40 min.). (c) Corresponding time-series in terms of absolute turning angle computed with a constant step length, $|\alpha_i^*|$, and smoothed speed, $\frac{L_i + L_{i+1}}{2\Delta t}$, segmented with M = 3 (leading to K = 15); the coloured bands appearing over the two time-series show the estimated occurrences and mean (plain horizontal line running in the middle of the band) +/- standard deviation (band width) for each of the three clusters considered.



4 Discussion

We showed that a generic method, segclust2d, that extends Lavielle (2005)'s and Picard et al. (2007)'s methods to bivariate time-series makes it possible to reliably detect two types of changes that are of key importance when studying animal movements: home range shifts, based on time-series of location coordinates (segmentation-only type), and changes in behavioural modes, based on time-series of turning angles and speed (segmentation-clustering type). In both types, this new method is straightforward to parameterise: the user has just to set the minimum segment length (Lmin) to a biologically

relevant value so as to prevent the time-series from being over-segmented. Nevertheless, it proved to work at least as well as, and often better than, other recent methods specifically designed to deal with either home range shifts (Gurarie et al. 2017) or changes in behavioural modes (Michelot et al. 2016; McClintock and Michelot 2018). As it can be applied to any bivariate signal, and can possibly be extended to deal with multivariate signals (if considering more than two time-series is required), our method appears to be a particularly appropriate tool not only in movement ecology but also in many other fields.

Breed et al. (2017) and Gurarie et al. (2017) independently developed an OUM-based method to identify home range shifts in mean location. Using computer simulations, we compared this approach, as implemented in Gurarie et al.'s quickfit algorithm, with segclutst2d/segmentation-only. We showed that, contrary to the OUM-based method, which can work only with a small and predefined number of shifts, our method works not only with any number of shifts but also estimate this number correctly by itself in most cases. In addition, when the number of shifts has been specified, only our method is able to correctly estimate the occurrences and timing of shifts in mean location (i.e. migration events) when these shifts are of small amplitude. Our method is also able to reveal changes in home range size. Yet, to be efficient, it simply requires specifying a minimum length (L_{min}) for stationary phase to be called a temporary home range, shorter phases being assumed to correspond to transitory exploitations of restricted areas rather than to home ranges. The elephant we considered in an illustrative example tended to commute between two main areas. This kind of space use is common in migrating birds that commute between reproductive and wintering home ranges. This is not necessarily the case, however, as an animal may use successively several temporary home ranges (Naidoo et al. 2012; Benhamou 2014; Cagnacci et al. 2016). The segmentation of a long piecewise locational time-series in phases corresponding to temporary home ranges opens promising perspectives to understand how the occurrences and durations of home ranges are related to environmental co-variates, which is a prerequisite to infer long-term consequences for population distribution (Mueller and Fagan 2008). The elephant illustrative example also shows that, although the model underlying segclust2d looks for stationary phases, there is no guaranty that all segments obtained are really stationary. This occurs because changes between stationary phases are modelled as breakpoints but may in fact correspond to slow progressive changes.

Since the pioneering paper by Morales et al. (2004; for more recent studies, see Breed et al. (2009, 2012); Langrock et al. (2012); McClintock et al. (2012)), HMM-based methods have often been considered the best way to detect changes in behavioural modes of remotely tracked animals. An alternative approach was proposed by Barraquand and Benhamou (2008). It consisted in computing the series of residence time within a virtual circle running along the path and to search for the most likely breakpoints using Lavielle (2005)'s univariate segmentation method. However, although the residence time provides a simple and reliable univariate signal easy to segment and interpret, the values obtained depend not only on the type of behaviour that is performed but also on how long it is performed, preventing the segments corresponding to the same behaviour from being easily clustered. In the present study, we show that the segclust2/segmentation-clustering

rivals a HMM-based method when applied to the bivariate signal provided by the two classical metrics that are linear and angular speeds. Importantly, such performance is reached without the need to specify any priors, whereas HMM-based methods can work only when fed with sufficiently informative priors. Better results were obtained with both methods when using other metrics such as the persistent and turning speeds (Gurarie et al. 2009; see also Gloaguen et al. 2015), and above all, the smoothed speed and the absolute value of the turning angles measured at constant step length, which were considered to improve the contrast between the modes. Using absolute rather than signed values not only works at best with our simulated movements even though right and left turns are balanced in any mode, but also presents the additional ability to fit well to area-concentrated searching phases that involve turning systematically right or left, i.e. characterized by markedly either negative or positive mean turning angles, as occurs in some species (e.g. Smith 1974).

In the illustrative example on zebra's movements, five behavioural modes were detected by segclust2d/segmentation-clustering in the time-series of smoothed speed and absolute value of the turning angles measured at constant step length. Nevertheless we chose to segment the time-series with only three modes – immobility, feeding and transit, as this sounded to us to be more biologically relevant. Indeed, although our method can estimate the number of states on a statistical basis as the most likely number of clusters, this estimate was not correct for a number of computer simulations whereas behavioural modes were clearly defined. With actual data, there can be some mixing between modes, for instance transit and opportunistic feeding at some times, so that the estimation of the number of relevant modes may become unreliable. Thus, we recommend using the capacity of segclust2d/segmentation-clustering to estimate the number of states only when this number cannot be fixed a priori based on biological arguments. A similar conclusion was reached by Pohle et al. (2017) for HMM-based methods. It is also worth noting that feeding and resting can be distinguished based on movement characteristics only in animals which have to move significantly (with respect to the location recording noise) to feed. For animals which feed mainly without markedly moving, such as some browser herbivores and carcass-eating carnivores, ancillary activity data are absolutely required to distinguish these two behavioural modes.

The segmentation of piecewise stationary time-series, possibly complemented by the clustering of the resulting segments into functional classes, is often key to understanding the dynamics of processes. Based on bivariate time-series of metrics such as location coordinates (northing and easting) or speed and turning angles, segclust2d has the potential to facilitate discovery in the field of movement ecology. If necessary, this approach could be easily extended to three and more dimensions, so as to consider ancillary variables such as temperature, activity (as provided by an accelerometer), distance to a nest, proxies of habitat quality, or any other variable that may be relevant when studying animal movements. Finally, as it can deal with two or more variables of any nature, our approach should be useful not only in movement ecology but also in many other fields.

Appendix 1: Complements about segclust2d

Expectation-Maximization algorithm and smoothing procedure

The Expectation-Maximization (EM) algorithm used to estimate the distribution parameters in the segmentation–clustering model is known to be sensitive to initialisation, so that it may converge to local maxima of the likelihood. This behaviour has some consequences on the parameters estimates but also makes the choice of the number of segments or states complicated. The classical initialisation solution consists in running the algorithm numerous times and just choose the point with the highest value of the log-likelihood, but this strategy is too computationally demanding. To minimize the risk of reaching local maxima within an unacceptable computation time, we propose the following initialisation strategy: (1) perform a pure segmentation of the signal and (2) use a hierarchical cluster algorithm, based on the log-likelihood ratio distance to assign segments to states.

Even with smart initialisation points, however, the EM algorithm may still converge to local maxima. This situation appears when looking, for a given number of states M, at the log-likelihood as a function of the number of segments K: whereas it is expected to be somewhat regular, this function can be quite noisy. To solve this issue, we propose to 'smooth' the function based on the parameter estimates of the distribution (π_m, μ_m, Σ_m) obtained for all the 'reliable' solutions, which correspond to the points that lie on the convex hull of log-likelihood curve, as smart initial points for any 'non-reliable' solution, i.e. for which an initialisation problem can be suspected. The improvement in terms of regularity of the log-likelihood curve obtained thanks to this procedure is illustrated in figure S1.1.

Model selection

Choice of the number of segments K in the pure segmentation model

We used the adaptive model selection strategy proposed in Lavielle (2005) consisting in choosing the value of K that maximizes the following penalized log-likelihood : $\mathscr{L}_\mathrm{K} - \mathrm{C}\,\mathrm{K}$ where $\mathscr{L}_\mathrm{K}$ is the log-likelihood of the optimal segmentation in K segments and C is a unknown positive constant to be calibrated. The heuristic proposed by Lavielle (2005) consists in detecting the value of K for which the log-likelihood ceases to increase significantly. More specifically, consider the normalised log-likelihood defined as

$$\tilde{\mathscr{L}}_\mathrm{K} = (\mathrm{K}_{max} - 1)\frac{\mathscr{L}_{\mathrm{K}_{max}} - \mathscr{L}_\mathrm{K}}{\mathscr{L}_{\mathrm{K}_{max}} - \mathscr{L}_1} + 1$$

Then, K is chosen as the value such that $\tilde{\mathscr{L}}_\mathrm{K}$ displays the largest slope change. Namely, we take :

$$\hat{\mathrm{K}} = argmin_\mathrm{K}\left\{(\tilde{\mathscr{L}}_\mathrm{K}\tilde{\mathscr{L}}_{\mathrm{K}+1}) - (\tilde{\mathscr{L}}_{\mathrm{K}+1}\tilde{\mathscr{L}}_{\mathrm{K}+2}) > \mathrm{S}\right\}$$

where the value of threshold S is set to a predefined value (we used S = 0.7 as proposed in Lavielle 2005).

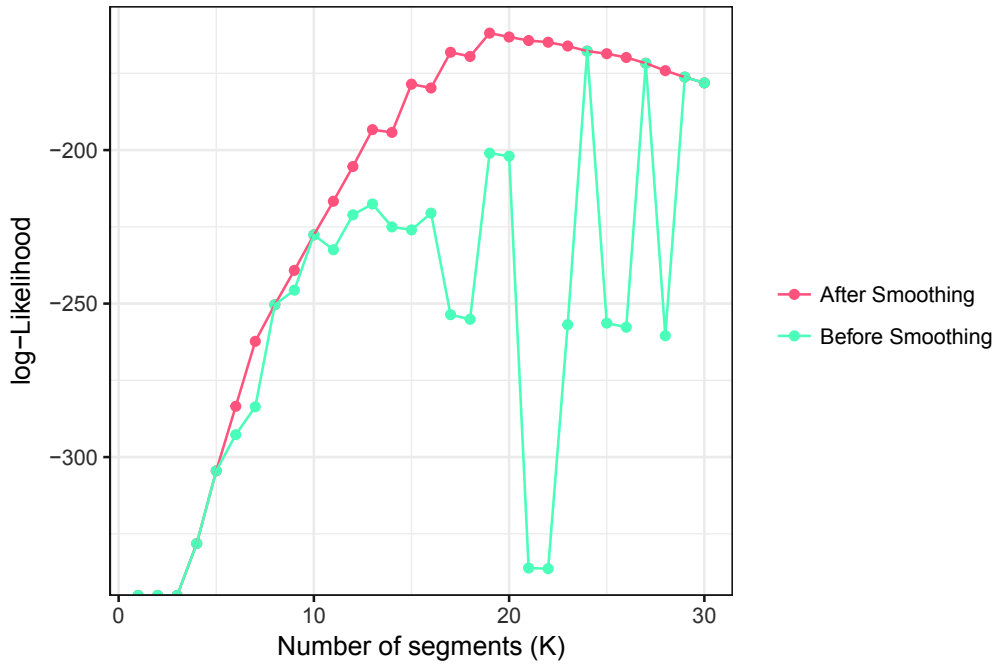


Figure S1.1 – Maximum Likelihood estimates as a function of the number of segments before (in blue) and after (in red) smoothing. For instance the 'reliable' solution obtained with K = 24 segments was used to provide starting points for the EM algorithm for K = 23 and for K = 25, and this smoothing procedure gradually spreads over adjacent points.

As the selection relies on a predefined threshold, it is worth checking where the point corresponding to the selected number of segment lies on a plot of the log-likelihood curve (fig. S3.2). The optimal K value obtained in this way should correspond to a noticeable slope change.

Choice of the number of segments K **and states** M **in the segmentation–clustering model**

Selection of the best segmentation-clustering model (i.e. of the best couple of K and M values) is a hard task as no method has been yet proposed for this purpose. A log-likelihood is expected to increase with the number of parameters. However, as explained in Picard et al. (2007), if the log-likelihood increases with the number of clusters M, it does not always increases with the number of segments *K*. Indeed a phenomenon of self-penalization occurs at the 'true' number of segments when the detection of breakpoints is easy, stressing to choose K simply as the value that maximizes the log-likelihood. However when the detection of breakpoints is more difficult, choosing the maximum value would tend to overestimate K. Picard et al. (2007) suggested to add a penalty. A Bayesian Information Criterion (BIC)-based penalty appeared to be sufficient in this case, although it does not work in pure segmentation (Picard et al. 2005). As BIC is the most popular criterion to choose the optimal number of clusters in a mixture model (Frühwirth-Schnatter 2006), we propose to use the maximum value of the following BIC-based penalised likelihood $\mathscr{B}_{\mathrm{K,M}}$ for the selection of both K and M parameters:

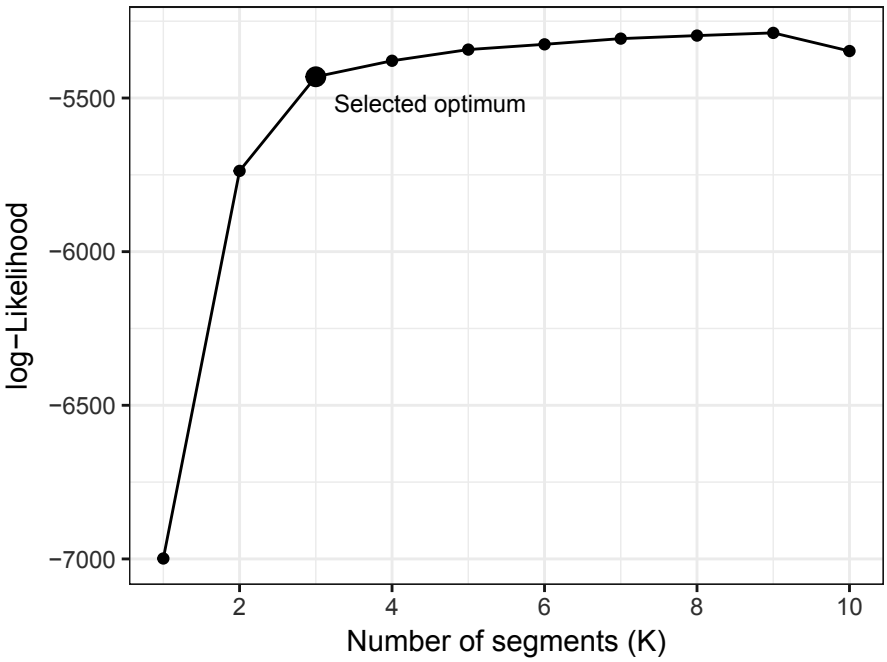


Figure S1.2 – log-likelihood of a segmentation as a function of the number of segment. The optimum selected by the criterion from Lavielle (2005) should be located at a break in the increase of the curve.

$$\mathscr{B}_{\mathrm{K,M}} = \mathscr{L}_{\mathrm{K,M}} - \frac{5 \times \mathrm{M} - 1}{2} log(2n) - \frac{\mathrm{K} - 1}{2} log(2n),$$

where $\mathscr{L}_{\mathrm{K,M}}$ stands for the log-likelihood for the optimal segmentation-clustering with K segments classified into M states. The penalization terms in the BIC criterion is half the number of parameters times the logarithm of the size of the dataset. For our model the number of parameters to be estimated is 2M means + 2M variances + M − 1 proportions for the states, and K − 1 breakpoints for the segments, and the size of the dataset for n bivariate values is $2n$.

Although this procedure appears to work well for choosing the optimal number of segments, it has been observed to be less reliable for choosing the optimal number of states, which tends to be overestimated. We therefore advise users to set an a priori number of states M, based on biological knowledge. We also advise to look at the plot of the BIC-penalized log-likelihood, as in figure 4b of main text, to check that the solution obtained makes sense.

Appendix 2: Interpolating entrance and exit points of a circle

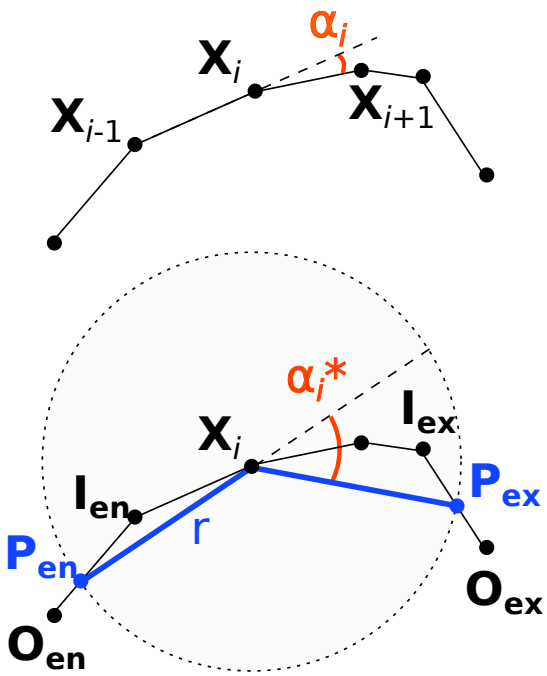


Figure S2.1 – Interpolating entrance and exit points of a circle.

Given a series of locations $\mathbf{X}_i = (x_i,\ y_i\ )$ recorded at constant time intervals Δt. Whereas turning angle at constant time intervals α_i (top) corresponds to the change in direction between vectors $\mathbf{X}_{i-1} \rightarrow \mathbf{X}_i$ (with length L_i) and $\mathbf{X}_i \rightarrow \mathbf{X}_{i+1}$ (with length L_{i+1}) and therefore act as a proxy for angular speeds $\left(\frac{\alpha_i}{\Delta t}\right)$, turning angle at constant length interval α_i^* (bottom) corresponds to the change in direction between vectors $\mathbf{P_{en}} \rightarrow \mathbf{X}_i$ and $\mathbf{X}_i \rightarrow \mathbf{P_{ex}}$, where $\mathbf{P_{en}}$ and $\mathbf{P_{ex}}$ are the last entrance and first exit locations, respectively, of a virtual circle with radius r and centred on current location $\mathbf{X}_i$. Let $\mathbf{I} = (x_{in}, y_{in})$ and $\mathbf{O} = (x_{out}, y_{out})$ be the last inside and first outside recorded locations, respectively, of the first passage at the circle perimeter, either backwards ($\mathbf{I} = \mathbf{I_{en}}$, $\mathbf{O} = \mathbf{O_{en}}$, $\mathbf{I_{en}} = \mathbf{X}_i$ if $L_i > r$) to determine $\mathbf{P_{en}}$, or forwards ($\mathbf{I} = \mathbf{I_{ex}}$, $\mathbf{O} = \mathbf{O_{ex}}$, $\mathbf{I_{ex}} = \mathbf{X}_i$ if $L_{i+1} > r$) to determine $\mathbf{P_{ex}}$. The location $\mathbf{P}$ (either $\mathbf{P_{en}}$ or $\mathbf{P_{ex}}$) corresponds to the point where the vector $\mathbf{I} \rightarrow \mathbf{O}$ intersects the circle perimeter. The length of this vector is $d_{IO} = (d_x^2 + d_y^2)^{0.5}$, with $d_x = x_{out} - x_{in}$, $d_y = y_{out} - y_{in}$, and its orientation is θ, with $\cos(\theta) = \frac{d_x}{d_{IO}}$ and $\sin(\theta) = \frac{d_y}{d_{IO}}$. In a new orthonormal frame of reference (U, V) originating at $\mathbf{I}$ and with U axis running through $\mathbf{O}$, the coordinates of current location $\mathbf{X}_i$ become $u_i = (x_i - x_{in})\cos(\theta) + (y_i - y_i n)\sin(\theta)$ and $v_i == (y_i - y_{in})\cos(\theta) + (x_i - x_i n)\sin(\theta)$. By applying Pythagoras' theorem, one gets $r^2 = (d_{IP} - u_i)^2 + v_i^2$, where d_{IP} corresponds to the distance between $\mathbf{I}$ and $\mathbf{P}$, with $d_{IP} > u_i$. Entrance or exit location can therefore be linearly interpolated as $\mathbf{P} = \mathbf{I} + (\mathbf{O} - \mathbf{I})\frac{d_{IP}}{d_{IO}}$ (i.e. $x_P = x_{in} + \cos(\theta) d_{IP}$ and $y_P = y_{in} + \sin(\theta) d_{IP}$), with $d_{IP} = u_i + (r^2 - v_i^2)^0.5$.

Appendix 3: Efficiency of the segmentation-clustering method

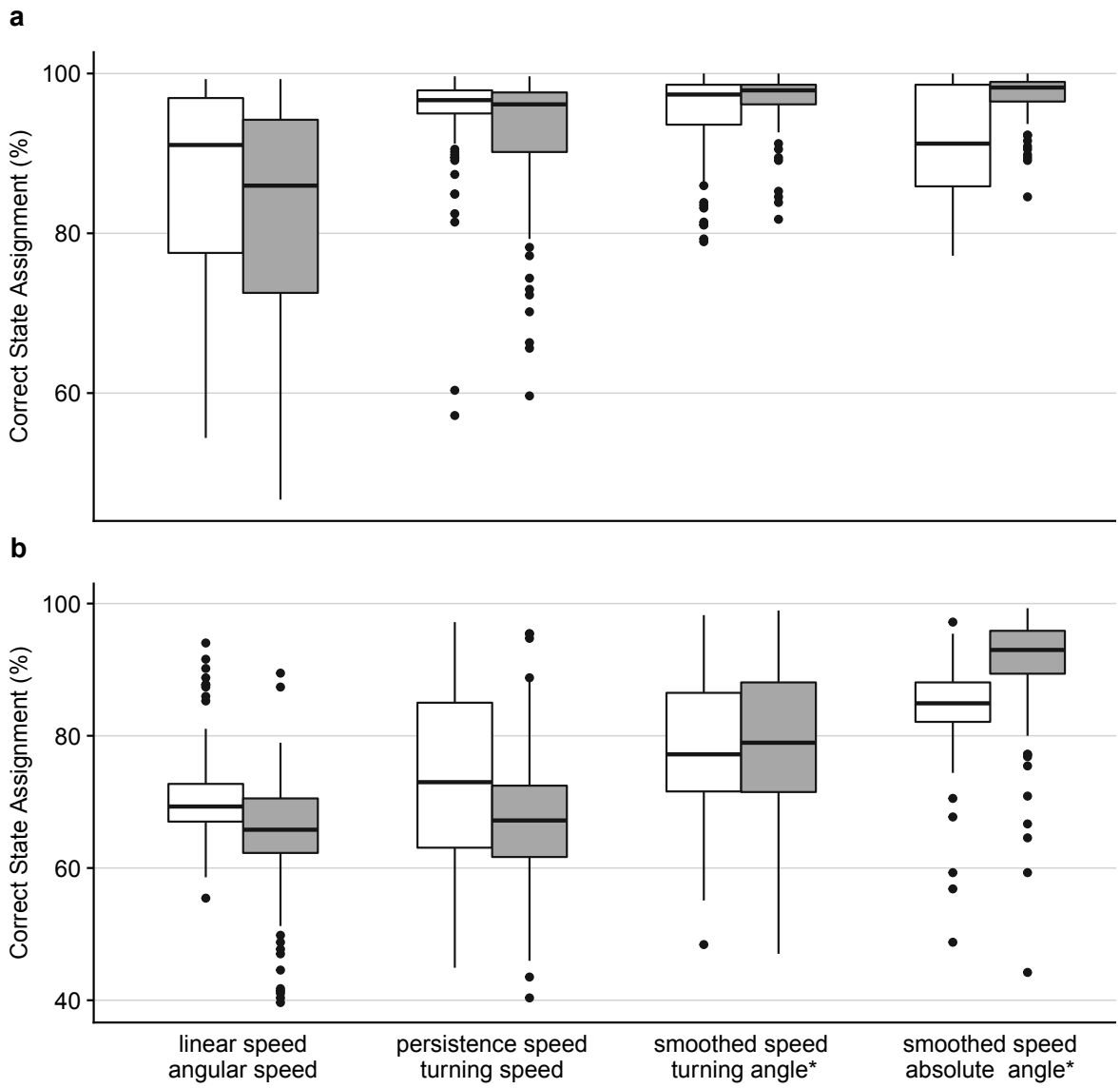


Figure S3.1 – Comparison with a HMM-based method for other additional noise levels: ζ = 0.25 u (a) or ζ = 0.35 u (b). The boxplots show the proportions of correct state assignments obtained using either (white boxplots) momentuHMM (McClintock and Michelot 2018), a HMM-based method specifically designed to deal with animal movements, with Gaussian priors set to the true means and variances of the various metrics in the different states, or (grey boxplots) our segclust2d/segmentation-clustering method, with L min = 10. The star (*) indicates turning angles computed with a constant step length, in arithmetic (α_i^*) or absolute value ($|\alpha_i^*|$). In any case, the number of states M was set to the true number of behavioural modes that were simulated (M = 3).

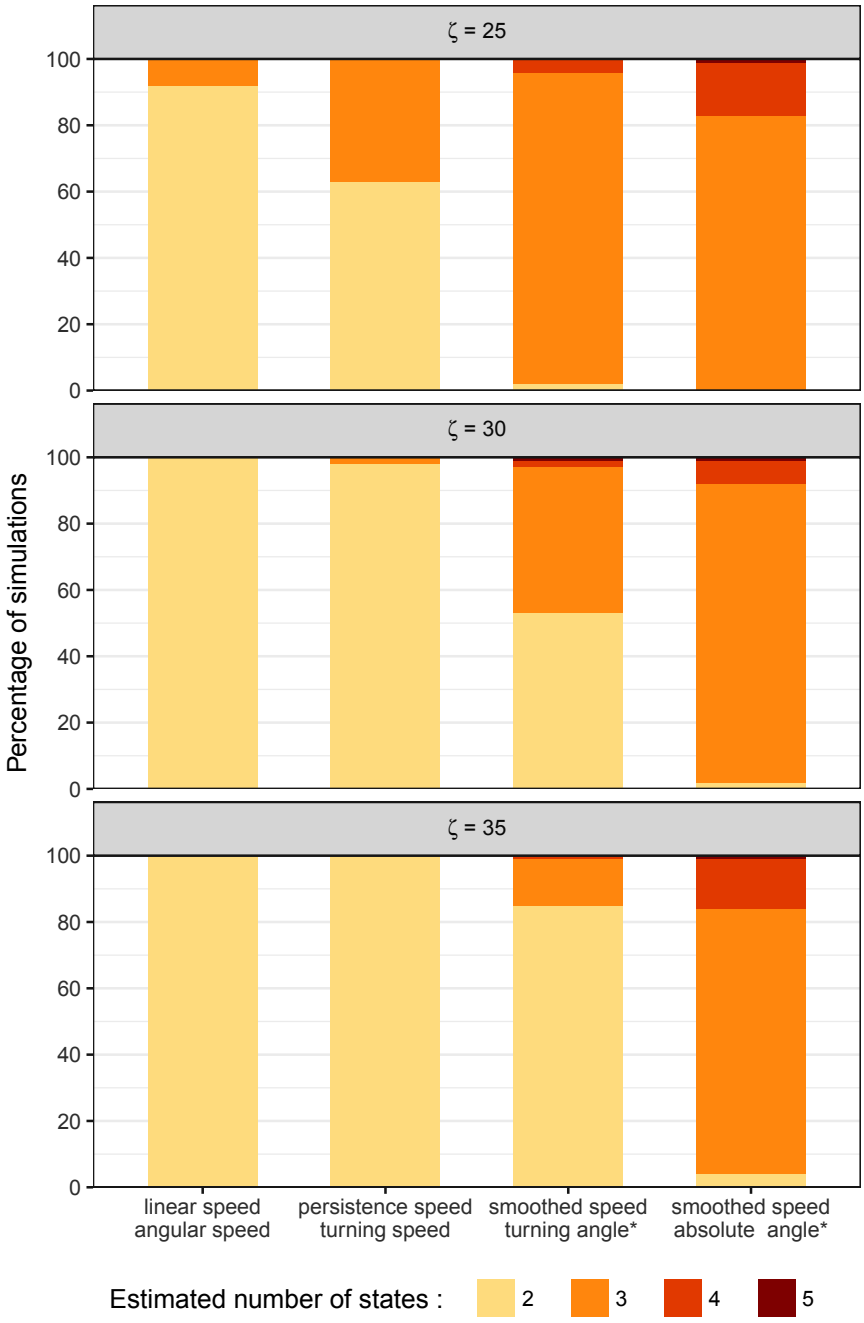


Figure S3.2 – Efficiency in the detection of the true number of states. The various bars show the proportions of simulations resulting in a predicted number of states equal to 2, 3, 4, or 5, for the three noise levels considered (ζ = 0.25 u, ζ = 0.30 u and ζ= 0.35 u) and the four types of couples of metrics considered. The true number of state is 3. The couple of metrics leading to best segmentation when the true number of states is known – absolute turning angle computed with a constant step length and smoothed speed – also leads to the best estimation of the number of states, but this latter estimation is not fully satisfactory, and should be worse with actual data because of possible mixing of movement behaviours.

Troisième partie

JEU SPATIAL ENTRE PRÉDATEURS ET PROIES

Chapitre 3

Optimal use of past information by enemies in the predator-prey space race

Utilisation optimale de l ’information dans la course spatiale prédateur-proie.

Rémi Patin, Daniel Fortin, Simon Chamaillé-Jammes

Article en préparation

Abstract

There is growing evidence that predators and prey can store knowledge of their previous experiences and that they use this information to determine where to move. A theory about how such information should be used to drive movement is however lacking, especially when considered within the spatial game played between predators and prey. To address these questions, we built a model predicting how individuals behaving optimally should use past information in a dynamic game between predators and prey. Our model provided insights on the importance of recent vs. long-term information about prey forage availabity and past predator-prey encounters. We used a genetic algorithm to find predator and prey optimal strategies in environment with different levels of heterogeneity regarding forage distribution and prey vulnerability. Optimal predators and prey use long-term information when the environment was heterogeneous. Expanding the concept of 'shell game', our model also highlighted that predators might benefit more than prey from ignoring past information and using random and unpredictable movements.

Contents

1 Introduction

As a pervasive interaction between organisms in nature, predation shapes many anatomical, physiological and behavioural traits of organisms. Among those traits, those influencing space and habitat use are key to the predation sequence (sensu Endler 1991), and can influence the encounter probability between predator and prey (Chapitre 2), the probability of detection by the predator (Mysterud and Østbye 1999), as well as the success of an attack (Hopcraft et al. 2005). Accordingly, understanding how predators and prey adjust their space and habitat use in response to each other has been a long-lasting goal for ecologists (Gilliam and Fraser 1987; Brown 1999; Laundré 2010).

Intuitively, at the larger spatial scale, predators and prey can be viewed as engaged in a space race. Prey should select patches offering good foraging opportunities while allowing to avoid predator (Gilliam and Fraser 1987; Abrahams and Dill 1989), whereas predators should select areas with high prey availability (Kacelnik et al. 1992; Kennedy and Gray 1993). The concept of the predator-prey space race has been continuously developed since the seminal work of Sih (1984), and covariation in the distributions of predators and prey can reveal whether predators or prey win the race. Predators win the space race when abundance of predators and prey are positively correlated in space, whereas prey win if the spatial correlation is negative. A general conclusion from theoretical and empirical studies is that the winner of the race is likely to be the one less spatially anchored to some specific areas for reasons unrelated to the predator-prey interaction (e.g., need to use specific, poorly distributed patches, presence of poorly mobile juveniles) (Sih 2005; Hammond et al. 2012).

Long-term spatial distributions of predators and prey at a population level are however an emergent pattern of a generally highly dynamics race occurring between individuals at much shorter temporal scales. A rapidly increasing number of empirical studies is revealing how predators and prey move at such fine scales (Fortin et al. 2005 ; Latham et al. 2011 ; Chapitre 2 ; Viejou et al. 2018), in particular thanks to the advances in biotelemetry (Cagnacci et al. 2010; Hebblewhite and Haydon 2010). It is now evident that predators and prey adjust their habitat selection and space use regularly and sometimes rapidly in response to changes in forage availability and predation risk (for the prey) (Latombe et al. 2014; Courbin et al. 2016) and changes in prey availability and catchability (for the predator ; Valeix et al. 2011). However, as the information and choices available to individuals are most often unknown to the researchers, the roles of memory and movement unpredictability in driving predator and prey movement remain unclear, although there is increasing evidence that they matter (Fortin et al. 2009; Avgar et al. 2015; Oliveira-Santos et al. 2016). Additionally, there is little theoretical work to guide studies conducted at these scales, as well as provide a foundation for theory-data feedback loops. This is particularly true when considering that theoretical works will be especially useful if they integrate both predators and prey response to each other (Lima 2002), a feature which is often lacking from current works.

Here we developed a model of predators and prey movement where both predator and prey movement strategies can evolve in response to the movement strategies of the other. We use this model to develop theoretical expectations about the role of unpredictable movement and use of past information in the predator-prey space race. We conceptually build on recent models and empirical studies emphasizing the importance of random-

ness as part of optimal predator and prey movement strategies, leading to the concept of 'shell game' (Mitchell and Lima 2002; Mitchell 2009; Laundré 2010). In the shell game, the predator tries to guess where the prey is located, while the prey tries to avoid the predator. Mitchell and Lima (2002) and Mitchell (2009)'s models showed that it could be advantageous for prey to be unpredictable by moving randomly between patches, but this was dependent on whether or not the predator memorized the past locations of its encounters with prey. Randomness in patch choice led prey to partially ignore the forage distribution, and this improved fitness only when the predator had the capacity to memorize past encounter locations. Indeed, in such situation, the predator would have been able to concentrate its search on prey-rich patches if those prey only focused on forage-rich patches and move predictably.

Few empirical studies have yet mentioned such processes (Gude et al. 2006; Fortin et al. 2009; Laundré 2010). Fortin et al. (2009) investigated group movement in american bisons (*Bison bison*) and found that smaller groups departed from meadow sooner. As smaller groups are more exposed to predation risk (Krause and Ruxton 2002; Lehtonen and Jaatinen 2016), they argued that they needed to more unpredictable in space, to avoid predation by wolves. Such risk from being predictable boils down to the importance of past information in driving the predator's space use. Thus, the role of predictability and use of past information in movement strategies likely interact, and ultimately determine the joint predator-prey movement strategies. Only a few models have investigated the importance of memory in driving movement (e.g. Bracis et al. 2015; Riotte-Lambert et al. 2015; Merkle et al. 2017) and even less have looked at its implication in the management of the food/safety trade-off (Bracis et al. 2018). Bracis et al. (2018) built a spatially explicit model where individuals could memorize resources and predators encountered, both of which were variable in space and time. They showed that prey using memory were more efficient at foraging and could better avoid predation, especially in situation where resources did not form clear and concentrated patches but were smoothly distributed. Otherwise predator were able to guard resources in a leapfrog effect (Sih 1998; Flaxman and Lou 2009). Although this highlights the importance of memory for prey, this however do not consider that predator could also respond to prey encounters and movement strategies (Lima 2002; Mitchell 2009). Moreover, Bracis et al. (2018) did not looked for the most efficient prey strategy but only compared pre-defined strategies, which could have been much different from optimal strategies, that evolution should favor.

Thus, under the realistic situation that both predators and prey adjust their behaviour to each other (Lima 2002), it remains unclear whether prey and predators should use past information on prey resource availability and encounters to determine their movement strategy, or whether unpredictability in movement should be more beneficial to them. We provide a theoretical framework to clarify expectations, focusing on the role of heterogeneity in the distribution of prey resources and vulnerability in balancing the costs and benefits of using past information and being unpredictable. In the model, predator and prey can choose among patches either randomly or according to their own past information of forage availability and previous encounters with a prey or a predator. Our model tries to answer several question about the use of information to drive movement, for both predator and prey and among different environmental conditions:

1. How important is information about forage availability compared to predator-prey encounters ?
2. Should information used to determine movement be based on recent or long-term knowledge ?
3. Is it beneficial to move randomly among patches ?

2 Methods

We combined a simulation model and a genetic algorithm (GA) to find optimal predator and prey movement strategies. The model, GA and analyses were implemented in R version 3.4.4 (R Core Team, 2018), using the Rcpp package (Eddelbuettel and François 2011; Eddelbuettel and Balamuta 2017).

2.1 Model outline

The model is briefly outlined here, and is described fully in the subsequent section. The model simulates the movement of a fixed number of predators and prey between a set of patches. Patches are characterized by (i) the current amount of forage available to the prey, which increases logistically over time but decreases with prey consumption, (ii) the maximum amount of forage that can exist in the patch and (iii) the vulnerability of prey if attacked by the predator or, equivalently, the success rate of attacks for the predator. At each time step prey forage and accumulate resources. When a predator is within a patch in which prey are also present, the predator has a probability of encountering a prey that increase with prey density. A predator attack only once per time step. The success of the attack depends on the vulnerability of the prey, which as said above is a characteristics of the patch. The fitness of the prey is determined by the resources accumulated weighed by its survival probability, given all encounters. The fitness of the predator is determined by the estimated number of prey consumed, i.e. the number of encounters weighed by the attack success of each encounters.

Current and past experiences within patches are used by both the prey and the predators to assign a given weight to each patch. Weights represent the assessment of patch quality from experience, and are therefore re-evaluated at each patch visit. Patches with more forage are given higher weight by the prey, and possibly also by the predators (to allow simulating the 'leap-frog' effect). Patches where the prey encountered the predator less frequently are given higher weights by the prey. Conversely, predators give higher weights to patches where they encountered prey more frequently. Predators and prey can give more or less weight to recent vs. old information, and information about patch quality can be more or less used to determine movement between patches.

In each run of the model predator and prey are assigned a strategy that controls how weights are evaluated and how patches are chosen. A strategy is defined by the values of 4 parameters (Table 1, and see 'Model formulation' section), which determine whether forage or encounters are more important in weighting patches, whether recent or past information about both forage and encounters is used, and finally whether patches are chosen according to the estimated weight or randomly.

Table 1 – Predator and prey strategy parameters

Symbol	Name	Description	Range	Eq.
β	Relative importance of information about encounter and forage availability	A low value of β leads individuals to use information about forage more than information about encounters when assessing patch quality	$[0.001 - \infty[$	3.9;3.10
δ	Use of long-term information about encounters	A low value of δ (~ 0) leads individuals to use information about encounters that occurred during the most recent time steps only. A very high value leads individuals to use information about all encounters, even old ones.	$[0.001 - 1e5]$	3.10
μ	Use of long-term information about forage availability	A low value of μ (~ 0) leads individuals to use information from the last visit only. A high value ($\mu \sim 0.99$) leads individuals to use information from all past visits.	$[0.001-0.99]$	3.8;3.12
α	Movement predictability	A low value of α (~ 0) leads individuals to move almost randomly among patches (unpredictable movement). A alpha value close to 1 leads individuals to choose patches according to their relative weights (predictable movement). A large value ($\alpha \sim 8$) leads individuals to almost always choose the patch with the highest weight (highly predictable movement).	$[0.001 - 8]$	3.14

Table 2 – Model parameters

Symbol	Definition	Equation	Value/Range
n_{pred}	Total number of predator		5
n_{prey}	Total number of prey		20
P	Total number of patches available		20
w_i	Weight of patch i, an estimate of its quality	3.1,3.2	$[0-\infty[$
f_i	Component of the weight linked to information about forage availability	3.1,3.2	$[0-\infty[$
e_i	Component of the weight linked to information about the probability of a deadly encounter with a predator (for the prey) or a successful capture of a prey (for the predator)(see below)	3.1,3.2	$[0-100]$
$intake_i$	prey resource intake	3.3	-
a	Prey attack rate of forage	3.3	0.08
h	Prey handling time of forage	3.3	0.75
R_i	Current forage available in patch i	3.5	$[0.1-K_i]$
n_i	Number of prey in patch i	3.3; 3.4	$[0-20]$
C_i	Total prey forage consumption in patch i	3.3; 3.4	$[0-K_i]$
K_i	Maximum forage or forage carrying capacity in patch i	3.3; 3.4;3.5	$[10-35]$
K_{min}	Minimum forage in a patch		0.1
r	Forage growth rate	3.5	0.2
E	Predator-prey encounter rate	3.6;3.7	0.1
n_e	Total number of predator-prey encounter	3.15;3.16	0-5 (prey), 0-1 (predator)
v_i	vulnerability of prey in patch i	3.9; 3.10; 3.15;3.16	0.001-0.2
v_{max}	Maximum prey vulnerability in the environment	3.9; 3.10	0.001-0.2

2.2 Model formulation

Predator and prey store estimates of the quality of each patch as weights. These weights are dependent on current and past information they have on both forage and encounters. The current weight of patch i is noted, for prey:

$$w_i = \frac{f_i}{e_i} \tag{3.1}$$

For predator:

$$w_i = f_i e_i \tag{3.2}$$

with f_i a component linked to information about forage availability, and e_i a component linked to information about the probability of a deadly encounter with a predator (for the prey) or a successful capture of a prey (for the predator)(see below).

At the beginning of the simulation, predators and prey are randomly distributed among patches, whose forage amount is set at the maximum value for each patch. Weights w_i and its component e_i and f_i are initialized with identical values for all patches. e_i are initialized to 1 for both predator and prey. For prey f_i are initialized to the mean forage intake among patches at the beginning. For predator, f_i is set to the mean forage availability among patches at the beginning. The model consists in a sequence of time steps, with updating of state variables within consecutive substeps.

Substep 1: Calculating prey forage consumption and forage renewal

This substep is repeated for all patches at each time step. Prey forage intake follow a type II response, providing there is enough forage in the patch to feed all prey present. Else forage is equitably shared among all prey present in the patch. Prey intake $intake_i$, in patch i, is calculated as follow :

$$intake_i = \frac{a\mathrm{R}_i}{1 + ah\mathrm{R}_i} \text{ if } \mathrm{R}_i > n_i \times intake_i \tag{3.3}$$

$$intake_i = \frac{\mathrm{R}_i}{n_i} \text{ else.}$$

with a the prey attack rate on forage, h the prey handling time, Ri the current amount of forage available in patch i, and n_i is the total number of prey in patch i.

Total forage consumption C_i by prey in patch i is then:

$$\mathrm{C}_i = n_i \times intake_i \tag{3.4}$$

Growth of forage in patches follow a logistic growth with a constant growth rate r, but a forage carrying capacity K_i that can change among patches. The amount of forage R'_i in patch i, is then updated as follow:

$$\mathrm{R}'_i = \mathrm{R}_i + r\mathrm{R}_i \left(1 - \frac{\mathrm{R}_i}{\mathrm{K}_i}\right) - \mathrm{C}_i \tag{3.5}$$

We imposed that a minimum amount of forage $\mathrm{K}_m in$ was always left in patches, so that no patch could stay without forage during the simulation.

Substep 2: Estimating encounters

For each patch where both predator and prey are present we repeat this substep for each predator. Each predator is sequentially presented each prey with a constant encounter probability (E). After the first encounter, the predator stops trying to encounter more prey. A prey can however encounter several predators. Formally the probability that a predator encounter a prey increase with the number of prey present in the patch $n_{prey,i}$:

$$Pr(encounter) = \sum_{j=1}^{n} E(1-E)^{j-1} = 1-(1-E)^{n} \tag{3.6}$$

The mean number of predator n_e encountered by a prey during a time step and given the number predator present in the patch $n_{pred,i}$ is thus :

$$n_e = n_{pred,i}\frac{(1-(1-E)^{n_{prey,i}})}{n_{prey,i}} \tag{3.7}$$

Visual representation of those functions may be found in Appendix 1, fig. S1.1 and S1.2.

Substep 3: Updating prey patch weight

For each prey, we update the weight given to the patch being currently occupied. Weights given to the other patches are not updated . The information about forage availability of patch i, f_i is updated to f_i' using the current intake realized in the patch:

$$f_i' = \mu f_i + (1-\mu) \times intake_i \tag{3.8}$$

μ therefore represents the balance between using recent information (with a low value of μ, f_i is mostly determined by current intake) and old information (with large value of μ, f_i is mostly determined by the long-term mean intake). μ ranges from 0.001 to 0.99.

Information about the probability of a deadly encountering with a predator e_i is updated to e_i' using the number n_e of encounters with predators during this time step and the vulnerability v_i in patch i.

$$\text{If } n_e > 0, \quad e_i' = e_i + n_e\beta\frac{v_i}{v_max} \tag{3.9}$$

$$\text{If } n_e = 0, \quad e_i' = e_i - \frac{\beta}{\delta} \tag{3.10}$$

Note that e_i is capped between 1 and 100. β measures by how much the probability of selecting a patch with the maximum vulnerability is divided. For other patches the probability is divided by $\beta\frac{v_i}{v_{max}}$. δ measures the number of time step in the patch without encountering a predator that is required so that an encounter during the current time step does not affect patch weight. For the other patches this time is actually $\delta\frac{v_i}{v_{max}}$. See appendix 2, fig. S2.1 for an example of how β and δ determine the dynamic of e_i. Finally, the updated weight w_i' is calculated following equation 3.7:

$$w_i' = \frac{f_i'}{e_i'} \tag{3.11}$$

Substep 4: Updating predator patch weight

For each predator, we update the weight given to the patch being currently occupied. This substep is very similar to substep 3 and here we only highlight what differs. Firstly, the updating of the information about prey forage availability f_i' is based on the amount of forage available in the patch , rather than on prey intake. Thus, we replace equation 3.8 by :

$$f_i' = \mu f_i + (1 - \mu R_i) \tag{3.12}$$

Secondly, e_i' is calculated using equation 3.9, as for the prey, except that the predator cannot encounter more than one prey. Thirdly, once f_i' and e_i' are obtained, the updated weights w_i' are calculated following equation 3.2 instead of equation 3.1:

$$w_i' = f_i' e_i' \tag{3.13}$$

Substep 5: Selecting target patches for predators and prey

At this stage, all patch weights w_i have been updated and can be used to determine in what patch do predators and prey move. This substep is therefore repeated for each predator and each prey. The probability of selecting patch i at the next time step is given by:

$$Pr(i) = \frac{w_i^\alpha}{\sum_{j=1}^{p} w_j^\alpha} \tag{3.14}$$

with α a parameter determining to what extent the choice of patches depends on the weights given to patches. If $\alpha \sim 0$, the individual chooses virtually randomly among patches, independently of the weights. If $\alpha = 1$, the probability for an individual of choosing a patch is proportional to its weight, relative to the weight of all other patches. If $alpha = 8$, the individual has a very high probability of choosing the patch with the highest weight. Actual strategies lie along a continuum between those cases.

Fitness calculations

At the end of the simulation the fitness of each predator and prey is calculated as follows. For each prey the fitness F_{prey} it is the product of the total intake and the survival probability:

$$F_{prey} = \left(\sum_{t=1}^{T} intake_t \right) \prod_{j=1}^{J} (1 - v_j) \tag{3.15}$$

With $intake_t$ the forage intake of the prey at time t, and v_j the prey vulnerability in the patch of the jth encounter, T the total number of time steps and J the total number of predator encounters.

For each predator the fitness F_{pred} is the mean number of prey consumed:

$$F_{pred} = \sum_{j=1}^{J} v_j \tag{3.16}$$

with J the total number of prey encountered and v_j the prey vulnerability in the patch of the jth prey encounter.

Note that encounters only affects fitness and no prey are ever removed from the simulation, are are interested in calculating optimal strategies given a population size. A prey can however have a very low survival at the end of the simulation.

2.3 Finding optimal strategies

To find the optimal strategies for both predator and prey, we built a genetic algorithm (GA) on top of the model (Hamblin 2013).The aim of a GA is to mimic the process of natural selection to explore efficiently a set of potential strategies and find the best one. This well-established approach is especially interesting when brute-force optimization using gradient of parameter values for all parameters across all combinations is not computationally feasible, which was the case for our model. GA relies on a balance between exploration through the generation of new strategies and exploitation through selection of good strategies (Hamblin 2013). The GA is initialized with a random set of strategies. For a given number of generations, we iterates the same operation: (i) the fitness of the set of strategies investigated is evaluated by running the model, (ii) strategies experiences selection and mutation, leading to a new set of strategies. First, strategies are selected. Selection is elitist, so the 10% best strategies are always kept for mutations. The other strategies are selected using the k-tournament method, with k = 2 (Hamblin 2013). The k-tournament is a non-parametric way of selecting the best strategies: we generate couples (if k = 2) of strategies and for each couple we keep the best one. After selection, each strategy parameter has a 5% chance of suffering mutations, which can be recombinations (2.5%), small mutations (1.25%) or large mutations (1.25%). Recombination replace the current parameter by the one of another strategy taken at random. Small mutations are small increment added to the current parameter value. Large mutation replace the current parameter by a new random value within the parameter range. On completion of the algorithm, a set of strategies remains and an additional series of generations is ran with selection but without mutation, in order to filter the remaining strategies until a single one remains for both predators and prey.

2.4 Analyses

We compared optimal strategies of predators and prey between four different types of environments that differ in the level of heterogeneity of forage and vulnerability among patches.

- Type 1: environments where maximum forage (K_i) and vulnerability (ν_i) are identical among all patches.
- Type 2: environments where vulnerability (ν_i) is identical among all patches while a quarter of patches have a higher maximum forage (K_i).
- Type 3: environments where maximum forage (K_i) is identical among all patches while a quarter of patches have a higher vulnerability (ν_i).
- Type 4: environments where a quarter of patches have a maximum forage (K_i) and a higher vulnerability (ν_i).

Each type of environment could however be characterized by different absolute values of maximum forage K_i or vulnerability ν_i, with each situation leading to only one optimal strategy for the predator and the prey. Therefore, for each type of environments, we found

optimal strategies for a number of specific situations, whose definition are found in Appendix 3, table S3.1. In the main Results section we present results aggregated by type to emphasize the general conclusions.

In addition to studying variations in optimal strategies among type of environments, we also examined the covariation, among types of environments, in parameter values for the prey and the predator strategies. We did so by conducting principal component analyses (PCA, Husson et al. 2017) on the values of the four parameters defining strategies – relative importance of information about forage and encounters, age of information about encounters, age of information about forage, movement predictability - separately for predators and prey. Similarly, we investigated whether values of parameters of predators and prey strategies were correlated between predator and prey. We did so by conducting a PCA on the table combining predator and prey parameter values.

3 Results

3.1 Movement predictability

In all types of environments, prey generally use past information more than predators to determine where to move (fig. 1a). Indeed, movements of prey were strongly biased towards patches having greater weight and therefore assessed as 'good' from past visits, i.e. where prey experienced less encounters with predators and performed better forage intake. Predator movement strategies involved much more randomness (fig. 1a). They did not bias strongly their movement towards patches assessed as 'good' from past visits, i.e. where predator experienced more encounters with prey and assessed better forage availability.

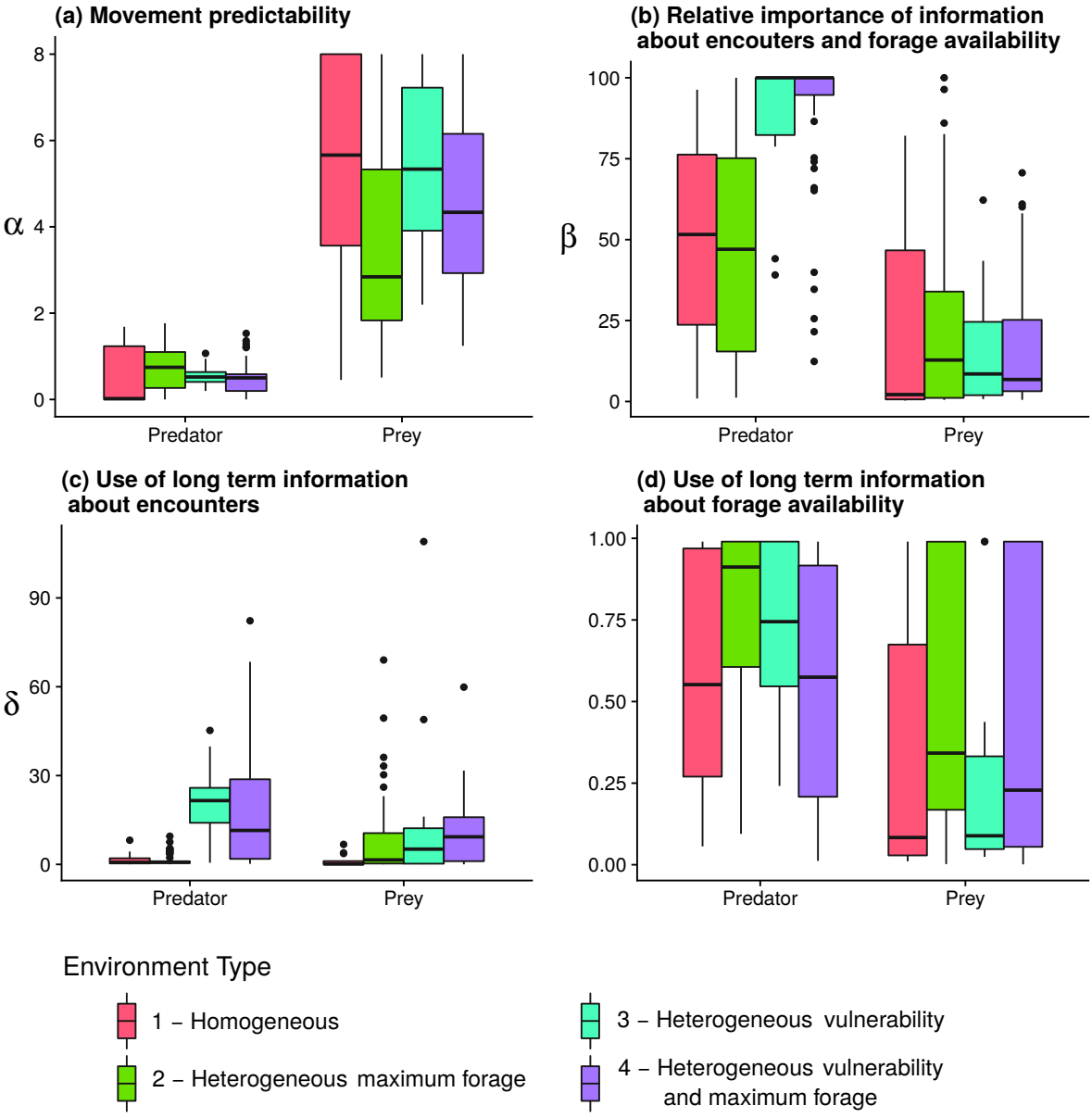
Relative importance of information about encounters and forage availability

Information about encounters had a greater importance for predator assessment of patch quality than for prey (fig. 1b). Predator relied more than prey on their past experience of encounters to estimate the quality of a patch. Predator used information about encounter even more when prey vulnerability was heterogeneous among patches (fig. 1b).

Is recent information about encounters more valuable than long-term ?

When prey vulnerability was heterogeneous, predator used older information about encounters than prey (fig. 1c, type 3 and 4), i.e. prey used more recent information about encounters compared to predator, which used more long-term information about encounters. When prey vulnerability was homogeneous and forage distribution heterogeneous, predator used mostly recent information about encounters, while prey also used older information about encounters (fig 1c, type 2). Finally, when both prey vulnerability and forage distribution were homogeneous, predator and prey relied mostly on recent information about encounters (fig 1c, type 1).

Figure 1 – **Optimal value for the different parameters under the different types of environment for predator and prey.** (a) α or movement predictability, low values correspond to random and unpredictable movement. High values correspond to movement directed towards the best patch, as estimated by the individual. (b) β, the relative importance of information about encounters and forage availability. (c) δ, the use of long term information about encounters. Low values correspond to the use of recent information. (d) μ, the use of long term information about forage availability.

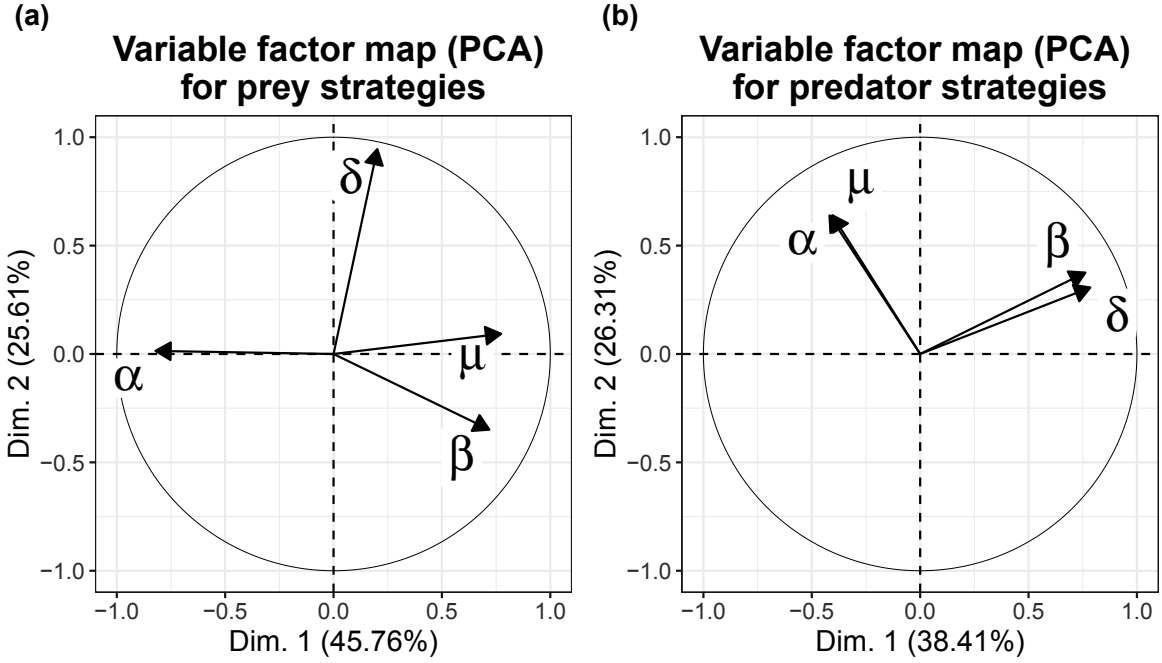


Is recent information about forage availability more valuable than long-term ?

Prey generally used more recent information about forage than predators (fig. 1d). When forage distribution was homogeneous, prey assessed forage availability in patches mostly based on their most recent visits (fig 1d, type 1 and 3). Older information and long-term intake rate contributed more to prey assessment when forage distrbution was

heterogeneous (fig. 1d, type 2 and 4). Predator assessment of forage availability in patches was mostly based on long-term information about forage (fig 1d).

Figure 2 – **Principal component analysis for (a) the prey strategies and (b) the predator strategies.** As a reminder, α is movement predictability, β is the relative importance of information about encounters and forage availability, δ is the use of long term information about encounters and μ, the use of long term information about forage availability.



Correlations among strategies

Principal component analyses of prey strategies among all environments indicated that there was no correlation between the use of long-term information about forage and encounters (fig. 2a, delta and mu). Prey that used more long-term information about forage availability displayed more unpredictable movement that relied less on past information (fig. 2a, α and μ). The importance of information about encounters was not associated to the use of long-term rather than recent information about encounter (fig. 2a, β and δ). Analyses of predator strategies showed a strong association between the predictability of movement and the use of long-term information about forage availability used (fig. 2b). Predator that assessed patch forage availability using long-term information had movement strategies more biased towards patch assessed as 'good'. Predator strategies also showed a strong association between the use of long-term information about encounters and its importance. Predator strategies relying on long-term information about encounters estimated patch quality by giving more importance to this information. Principal analyses of both predator and prey strategies did not show strong covariation of predator and prey strategies (see Appendix 4, fig. S4.1).

4 Discussion

We developed, to our knowledge, the first model predicting how both predator and prey should use random movement and past information about forage and encounters. Memory and randomness have already been identified to shape movement response to predation (Avgar et al. 2015; Viejou et al. 2018; Fortin et al. 2009). Theory has however been lacking on these aspects. Our model sheds light into how past information about resources and predation should be used to drive movement. It also highlight the importance of being unpredictable in the predator-prey spatial game.

Therefore, our model provides insights on the cost and benefits of randomness in the predator-prey spatial game. Previous models (Mitchell and Lima 2002; Mitchell 2009) had already developed the idea of a shell game played between the predator and the prey, in which both the prey and the predator would benefit from moving somewhat randomly in the landscape. Random movement by prey could reduce the the searching efficiency of predators that can memorize past encounters and could use this information for later searches (Mitchell 2009). Random movement by prey however entails that prey do not focus on the most rewarding foraging patches, and thus entails costs related to lost foraging opportunities. In our model those cost may be even more important because patches were subject to depletion and shared among all prey. Under the different environments tested in our model, randomness was no longer beneficial and prey strategy involved movement highly directed towards the patches assessed as favourable in previous visits. When randomizing their movement and therefore ignoring both information on forage and predator encounters, prey faced two different costs : they risked visiting patches highly used by predators or with lower forage intake. In most circumstances, these different costs largely outweighed the potential benefits of being unpredictable to the predator. On the other hand, predator did benefit in most environments from having rather unpredictable use of patches. Even though predator could select both for patches with higher forage and more encounters, the cost of ignoring this information is likely to be lower than for the prey, as forage do not affect directly predators and is just a potential proxy for prey presence (Flaxman and Lou 2009). In opposition to a prey, a predator that visits a patch with lower forage do not directly suffer from missed opportunity cost. These costs are therefore outweighed by the benefit for predators of being unpredictable to the prey, leading predators to use more random movement, while partly ignoring past information about forage and encounters. With this model, we confirm the potential importance of randomness in the predator-prey spatial game, but emphasize and explain why we should expect prey to be more predictable than predators

Our model also improve our understanding of how past information should be used to drive movement in a predator prey spatial game. There are numerous empirical evidence that predator and prey movement respond to prey resources and vulnerability (Fortin et al. 2005; Balme et al. 2007; Creel et al. 2005; Latombe et al. 2014; Basille et al. 2015). There are also growing evidence for the use of memory in driving movement (Wolf et al. 2009; Oliveira-Santos et al. 2016). This suggest that predator (or prey) may perfectly well use cognitive maps of the distribution of prey (or predator), forage availability and prey vulnerability to inform they movement. It remains however unclear how such information should be used. In our model we provide insight on how recent and long-term information may be useful in different environmental context. This distinction between

recent information and long-term information can also be linked to the different component of memory. Using recent information may represent the importance of the working (or episodic) memory while using long-term information may represent the importance of the reference memory (Bailey et al. 1996; Bennett and Tang 2006; McLane et al. 2011).

In general, our model emphasize the link between the heterogeneity of the environment and the importance of long-term information in driving patch choice. Indeed, predator and prey granted higher importance to long-term information about encounters when prey vulnerability was heterogeneous. Prey valued long-term information about forage information when maximum forage was heterogeneous and predator did so when vulnerability was homogeneous but maximum forage heterogeneous. Thus, in our model, heterogeneous environments generally favored the use of long-term information – or reference memory – in determining patch-use. The use of long-term information was however not linked between encounters and forage availability. It could be beneficial for predator or prey to use recent information about forage availability but long-term information about encounters. Our findings extend the few empirical evidence (Shumway 2010; White and Brown 2014) and theoretical development (Fagan et al. 2013) that environmental heterogeneity favors the evolution of memory.

In conclusion, we proposed a model of the predator-prey spatial game which can predict the benefits of movement unpredictability, as the relative value of recent versus long-term information about forage availability and encounters in driving patch choice. We advocate the use of genetic algorithm for its potential in solving complex predator-prey game. Our model emphasized the importance of environmental heterogeneity in favoring the value of long-term information. In contrast to previous works (Mitchell and Lima 2002; Mitchell 2009), our results highlighted the benefits for predator of being unpredictable and the importance for prey to use predictable movement directed toward resources while avoiding predator. Based on this investigation, we predict that movement of prey should be more predictable than movement of their predator, a prediction that is open to empirical investigations.

Appendix

Appendix 1. Graphical representation of encounter probabilities

Figure S1.1 – **Probability that a predator encounter a prey given the number of prey in the patch**

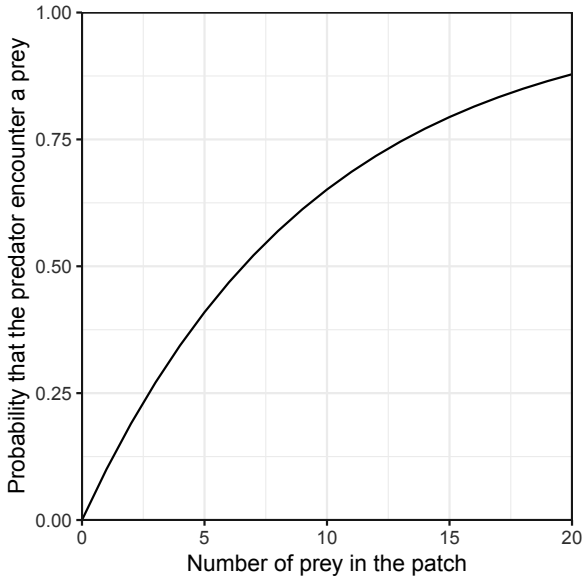
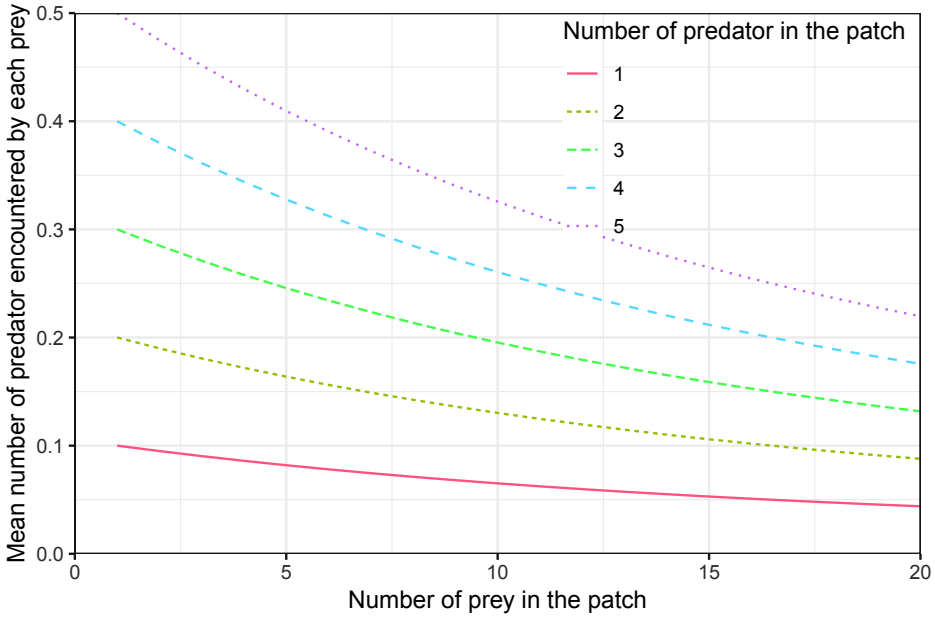
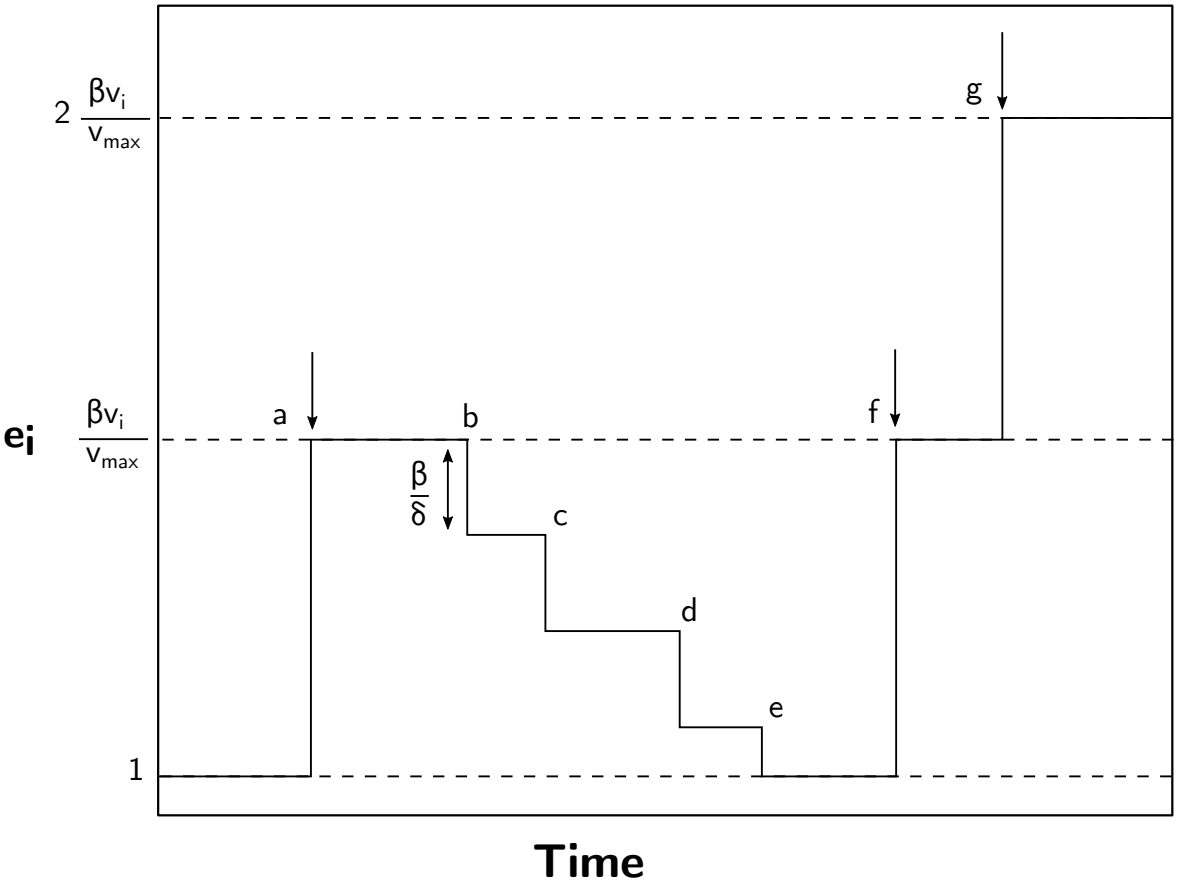


Figure S1.2 – **Mean number of predator encountered by a prey given the number of prey and predator in the patch**



Appendix 2. Example of weight dynamic

Figure S2.1 – **An exemple of the dynamic of the component e_i of the weight in a given patch.** e_i represent an estimation of the probability of a predator-prey encounter in the patch. Here the patch is visited 7 times by the individual during this interval, at time a to g. 3 predator prey encounter occurred, at time a, f and g, as symbolized by the arrows.. At those time, e_i immediately increase by a constant number $\beta\frac{v_i}{v_{max}}$ that depends on the prey vulnerability in the patch and the individual strategy β. For the other visit, without any predator-prey interaction, e_i decrease by a fixed amount, $\frac{\beta}{\delta}$. Here, after 5 visits, e_i return to its baseline value. This means that $\delta\frac{v_i}{v_{max}} \sim 5$ in this patch. Note that e_i cannot be greater than 100.



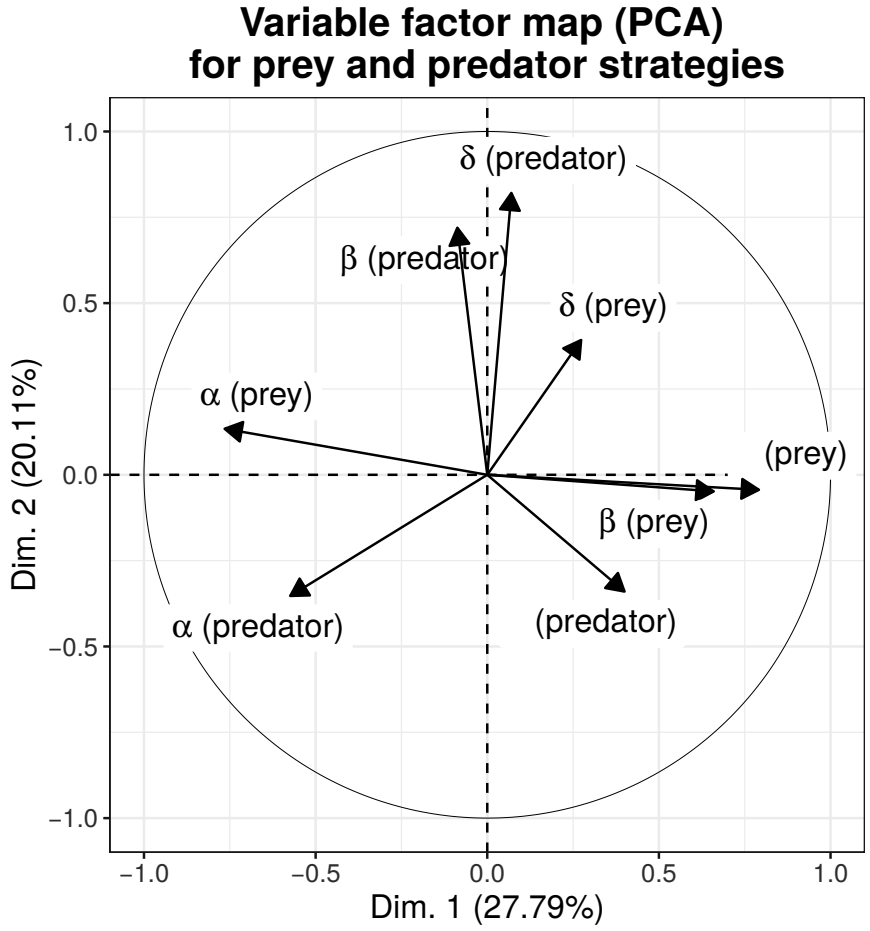
Appendix 3: Definitions of environment types.

Values assigned for the different environment type. n is the number of environment of each type.

Type	Maximum forage	Vulnerability	Maximum forage in patch i		Vulnerabaility in patch i		n
			Standard patch	Richer patch	Standard patch	Riskier patch	
1	Homogeneous	Homogeneous	10,15	-	0.001, 0.002, 0.005, 0.01, 0.02, 0.05, 0.1, 0.2	-	16
2	Homogeneous	Heterogeneous	10, 15	-	0.001	0.002, 0.005, 0.01, 0.1	16
					0.01	0.02, 0.05, 0.1	
					0.1	0.2	
3	Heterogeneous	Homogeneous	10	15, 20, 25, 30	0.001, 0.002, 0.005, 0.01, 0.02, 0.05, 0.1, 0.2	-	56
			15	20, 25, 30			
4	Heterogeneous	Heterogeneous	10	15, 20, 25, 30	0.001	0.002, 0.005, 0.01, 0.1	56
					0.01	0.02, 0.05, 0.1	
			15	20, 25, 30			
					0.1	0.2	

Appendix 4. PCA among predator and prey strategies

Figure S4.1 – **Principal component analysis between both prey and predator strategies.** As a reminder, α is movement predictability, β is the relative importance of information about encounters and forage availability, δ is the use of long term information about encounters andμ, the use of long term information about forage availability.



DISCUSSION

Dans cette thèse, je me suis intéressé à l'importance du déplacement dans l'interaction prédateur proie. À travers l'utilisation de l'espace qu'il génère, le déplacement est un comportement transversal à la séquence de prédation que l'on a présenté dans l'introduction (fig. 1 ; Endler 1991). Il intervient en effet à la fois dans les étapes de rencontre, de détection et d'attaque. Le déplacement est susceptible d'interagir avec les comportements intervenant dans ces différentes étapes. Cette thèse a permis d'avancer notre connaissance de ces interactions et de développer l'importance du déplacement dans l'étape de rencontre.

Résumé des chapitres et résultats

Dans le Chapitre 1, j'ai exposé un modèle théorique pour montrer l'importance de la prise en compte du déplacement et de l'utilisation de l'espace dans les études impliquant la vigilance et la taille du groupe. En effet si la vigilance permet de gérer le compromis risque/ressources, l'utilisation de l'espace est généralement un autre moyen d'y parvenir si jamais risque et ressources sont spatialement associés. Dans ce cas, les proies peuvent ajuster leurs investissements anti-prédateurs en augmentant leur vigilance et en diminuant leur taux d'acquisition de ressources ou alternativement en allant dans des endroits moins risqués mais disposant de moins de ressources. Le modèle présenté s'applique à des groupes sociaux de taille fixe dans lesquels un meneur décide de l'utilisation de l'espace selon son intérêt propre et les autres individus suivent ses décisions. Tous les individus sont à même d'ajuster leur niveau de vigilance en fonction de la situation. En utilisant un algorithme de programmation dynamique (Houston et al. 1988), on a pu obtenir les stratégies optimales des différents individus en fonction de leurs conditions nutritionnelles. Dans les modèles classiques de vigilance, les proies dans les groupes plus grands, qui bénéficient d'un effet de dilution, diminuent généralement leurs investissements anti-prédateurs et donc leur vigilance. On obtient alors une décroissance de la vigilance avec la taille du groupe. Dans le modèle présenté, en autorisant les meneurs à ajuster aussi l'utilisation de l'espace du groupe, on n'observe plus de relation simple entre la vigilance et la taille de groupe. De plus, les autres individus du groupe, les suiveurs, ne participant pas aux décisions spatiales, pâtissent de réserves d'énergie plus faibles car ils sont incapables d'aller dans la parcelle riche en ressources lorsque leur condition se dégrade. Pour compenser cette perte de condition, les suiveurs diminuent leur vigilance et peuvent ainsi anticiper les futures incertitudes concernant l'acquisition de ressources. Ils subissent donc un risque de prédation plus élevé que les meneurs. Malgré ces risques augmentés, les suiveurs bénéficient quand même de l'effet de dilution du groupe et montrent qu'ils peuvent vivre plus longtemps que s'ils étaient solitaires et à même de décider eux-mêmes de leur utilisation de l'espace, mais sans bénéficier d'un effet de dilution. Dans les Analyses complémentaires du Chapitre 1, j'ai présenté un exemple empirique d'ajustement de l'utilisation de l'espace à la taille de groupe chez le zèbre des plaines. Dans la population de Hwange, Zimbabwe, les groupes de taille plus importante ont tendance à utiliser des zones où la densité d'utilisation par les lions est plus élevée.

Dans le Chapitre 2, j'ai présenté le fruit d'une collaboration : nous nous sommes intéressés aux stratégies spatiales chez le zèbre des plaines et à l'importance du déplacement dans l'étape de rencontre. Dans ce chapitre, nous avons mis en évidence l'existence de migrations quotidiennes des zèbres lesquels s'éloignent, chaque nuit, des points d'eaux où se concentre leur risque de prédation. Durant le jour, les zèbres sélectionnent les larges parcelles de milieu ouvert proche des points où ils peuvent bénéficier du fourrage et d'une détection accrue des prédateurs. Au crépuscule, quand les lions deviennent actifs, les zèbres s'éloignent des points d'eau de quelques kilomètres réduisant ainsi fortement leur probabilité de rencontre avec leur prédateur, les lions restant auprès des points d'eau. Les zèbres révèlent aussi des changements dans leur sélection des différents habitats, mais ces changements participent pour très peu à la réduction du risque de rencontre avec les lions, si on les compare aux migrations quotidiennes. Dans les Analyses complémentaires du Chapitre 2, je présente quelques données de vigilance relevées sur le terrain pour essayer de comprendre les activités quotidiennes chez le zèbre et de vérifier si les investissements anti-prédateurs varient au cours de la journée.

Dans le Chapitre 3, j'ai continué d'étudier le rôle du déplacement dans l'étape de rencontre en m'appuyant sur les possibilités de la mémoire pour expliquer comment les déplacements peuvent affecter les probabilités de rencontre indépendamment des questions d'habitat. J'ai donc construit un modèle théorique, utilisant un algorithme génétique, pour prévoir les stratégies optimales des prédateurs et des proies. Dans ce modèle, les prédateurs et les proies pouvaient se servir de leur mémoire pour diriger leurs déplacements vers les parcelles offrant davantage de fourrage. Ils disposaient aussi d'une mémoire des rencontres précédentes avec l'autre joueur qui pouvait rendre attractives pour les prédateurs ou répulsives pour les proies les parcelles concernées par les rencontres. Prédateurs et proies pouvaient aussi choisir d'utiliser seulement les informations récentes dont ils disposent ou bien leurs connaissances à plus long-distance pour diriger l'effet du fourrage et des rencontres dans leur sélection des parcelles. Les joueurs pouvaient enfin choisir d'ignorer plus ou moins leurs connaissances sur les différentes parcelles afin de sélectionner plus ou moins aléatoirement les parcelles utilisées. Les stratégies optimales ont ensuite été évaluées pour des environnements différant par l'hétérogénéité de la répartition du fourrage et de la vulnérabilité des proies. Les précédents modèles s'intéressant à l'utilisation de la mémoire et de l'imprévisibilité chez les prédateurs et les proies (Mitchell and Lima 2002; Mitchell 2009) ont conclu à l'intérêt pour les proies de se montrer imprévisibles – c'est à dire de se déplacer aléatoirement – face à des prédateurs capables de mémoriser l'emplacement de leurs précédentes rencontres. Dans le modèle du Chapitre 3, cependant, les stratégies optimales des proies impliquaient généralement des déplacements fortement dirigés par la mémoire passée des rencontres et du fourrage précédemment observé dans les parcelles visitées. À l'inverse les stratégies des prédateurs impliquent généralement des déplacements plus aléatoires, rendant leur répartition spatiale difficile à anticiper pour les proies. L'hétérogénéité de la répartition du fourrage et de la vulnérabilité était souvent liée à l'utilisation d'information à long-terme respectivement vis à vis du fourrage et des rencontres proies-prédateurs, et ce chez les prédateurs et les proies. Lorsque la vulnérabilité des proies était spatialement hétéro-

gène, les prédateurs accordaient une plus grande importance aux rencontres passées par rapport à leur connaissance de la répartition du fourrage pour décider des parcelles qu'ils utilisaient. Le modèle a aussi permis de mettre en avant les associations entre stratégies à travers les différents environnements. Par exemple, les prédateurs et proies utilisant l'information à long-terme par rapport à la répartition du fourrage, n'utilisaient pas pour autant, concernant les rencontres prédateur-proie, une information à long terme. On a aussi pu mettre en évidence que les proies se déplaçant de manière plus imprévisible utilisaient leurs connaissances de la répartition du fourrage à plus long-terme. Les prédateurs accordant plus d'importance aux rencontres passées par rapport à leurs connaissances du fourrage utilisait l'information liée aux rencontres passées à plus long terme. Avec ce modèle, je propose un premier cadre permettant de déterminer comment l'information à propos des rencontres passées et de l'environnement doit être utilisée dans un jeu spatial prédateur-proie.

L'importance de la prise en compte des interactions comportementales

Les comportements spatiaux sont essentiels dans l'interaction proie-prédateurs et leurs effets ont été démontrés de nombreuses fois (Gorini et al. 2012; Gilliam and Fraser 1987; Brown 1999). Ils interviennent cependant conjointement avec l'ensemble des comportements qui affectent la probabilité et l'issue des rencontres proie-prédateur. Pour pouvoir résoudre les différents compromis auxquels une proie fait face et donc pouvoir estimer et prévoir ses investissements dans les comportements anti-prédateurs, il faut pouvoir appréhender l'ensemble des comportements possibles et leurs interactions. Les comportements spatiaux étant particulièrement transversaux dans la séquence de prédation (voir fig 1, ombrage) et affectant généralement de manière simultanée les phases de rencontre, de détection et d'attaque, ils sont particulièrement propices aux interactions. Dans cette thèse, j'ai mis en évidence deux interactions entre les comportements spatiaux et les autres comportements anti-prédateurs : dans le Chapitre 1, une interaction avec la vigilance et la taille de groupe et dans le Chapitre 2, une interaction avec les rythmes d'activité circadiens.

Grégarisme et ajustement des investissements anti-prédateurs

L'interaction entre vigilance et taille de groupe a été étudiée de longue date (Lazarus 1978; Bertram 1980; Elgar 1989; Roberts 1996). Il a été souvent observé que la vigilance diminuait avec la taille de groupe (Beauchamp and Ruxton 2008; Beauchamp 2001, 2017). Les effets de détection et de dilution sont les principales explications de cette diminution (cf introduction). L'idée est que la socialité diminue le risque de prédation et permet donc à la proie de réduire ses autres investissements anti-prédateurs, c'est à dire sa vigilance, pour bénéficier d'un taux d'acquisition de ressources accru. Si ce raisonnement fonctionne pour la vigilance, il peut aussi être appliqué pour n'importe quel autre com-

portement anti-prédateur. C'est ce que montre en effet le modèle du Chapitre 1, pour lequel on a pris en compte la possibilité pour un individu d'utiliser des milieux plus ou moins risqués et associés à plus ou moins de gain en ressources – ce qui est représenté dans le modèle par deux parcelles, l'une riche et risquée, l'autre pauvre mais sûre. Lorsqu'on prend en compte la possibilité pour la proie d'investir dans deux comportements anti-prédateurs différents, la vigilance et l'utilisation de l'espace, alors, le comportement optimal des proies n'est pas nécessairement de diminuer la vigilance lorsque la taille de groupe augmente. Par contre, les proies doivent, lorsque la taille de groupe augmente, diminuer leur investissement total dans les comportements anti-prédateurs, ce afin de bénéficier de la réduction du coût de ces comportements, c'est à dire ici de l'augmentation du taux d'acquisition des ressources. Cela sera possible si la diminution des coûts (par ex. l'acquisition accrue de ressources) liés à l'utilisation plus faible du comportement anti-prédateur (par ex. la vigilance) produit un bénéfice supérieur à l'augmentation du risque concomitante (voir fig. 3). Ce raisonnement peut s'appliquer pour la vigilance, l'utilisation de l'espace et n'importe quel comportement anti-prédateur ou combinaison de comportements. Si les comportements sont plus nombreux cependant la résolution du compromis n'est pas toujours triviale.

Si les exemples de diminution de la vigilance avec la taille de groupe sont nombreux (Elgar 1989; Roberts 1996; Beauchamp and Ruxton 2008), nous n'avons pas beaucoup de données pour d'autres comportements. Ainsi en est-il de l'utilisation de l'espace : très peu d'études empiriques se sont intéressées à ce sujet (Krause et al. 2000; Fortin et al. 2009; Murthy et al. 2016) , avec des méthodes, des taxons différents et des résultats contrastés. Krause et al. (2000) ont travaillé sur des épinoches et ont mené une expérience pour voir comment l'utilisation d'un refuge changeait avec la taille de groupe et la taille du corps. Ils ont observé que les grandes épinoches, moins contraintes par les ressources que les petites, émergeaient plus tôt des refuges lorsque la taille du groupe augmentait. Si les résultats sont cohérents avec l'hypothèse d'une diminution de l'investissement anti-prédateurs dans les refuges lorsque la taille de groupe augmente, ils pouvaient aussi être expliqués par la compétition accrue pour les ressources ou par la plus forte probabilité de présence d'individus téméraires qui entraîneraient les autres individus lorsque la taille de groupe augmente Krause et al. (2000). De plus, l'utilisation de l'espace est ici étudiée dans un contexte très spécifique (utilisation d'un refuge, à très fine échelle) et pour une durée très courte (expérience de quelques minutes) qui ne permet pas de considérer les ajustements à plus long terme.

Murthy et al. (2016) ont pour leur part travaillé avec des larves de moustiques (*Aedes aegypti*, 'yellow fever mosquito'). Ils ont regardé à partir d'une expérience comment des groupes de moustiques utilisaient deux types de milieux, plus ou moins risqués, représentés par deux moitiés de boîte de pétri plus ou moins sombres, la partie sombre étant moins risquée du fait de la difficulté accrue de détection des larves à l'intérieur. Leurs résultats montrent que lorsque la taille de groupe augmente, les larves utilisent davantage les milieux moins risqués, ce qui est à l'opposé de l'hypothèse originelle. Cette différence peut s'expliquer de deux manières. D'abord lorsque les larves sont plus nombreuses, elles sont potentiellement beaucoup plus voyantes dans le milieu clair et risqué qu'une larve

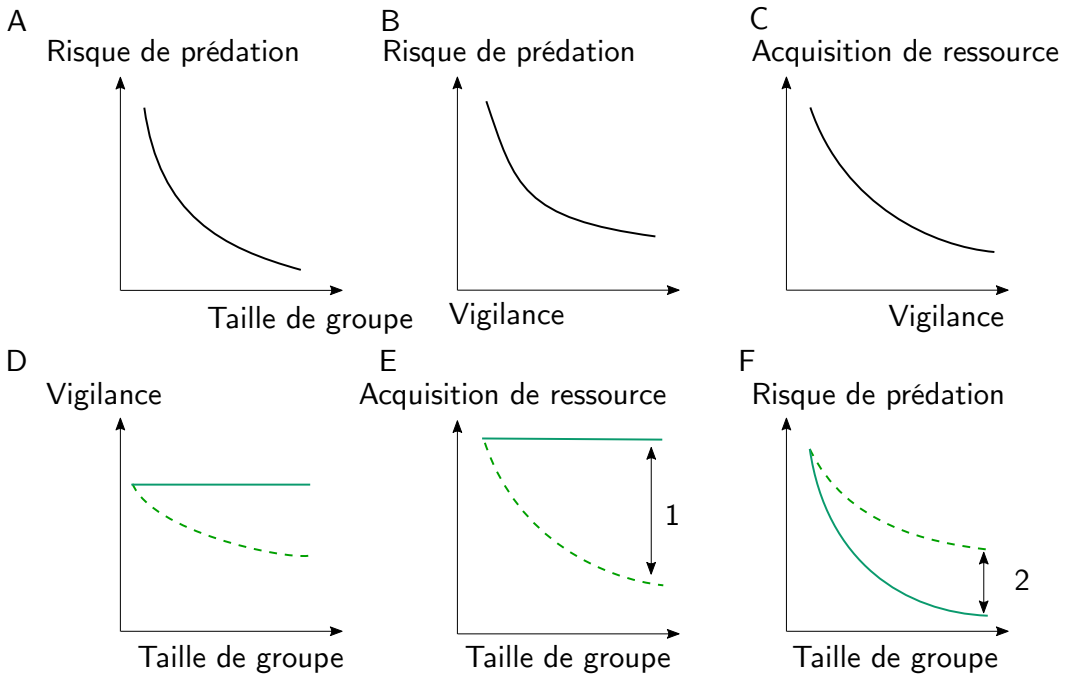


FIGURE 3 – **Effet de dilution de la taille de groupe.** Cette figure présente les hypothèses nécessaires pour observer une interaction entre la taille de groupe et d'autres comportements anti-prédateur. A. Le risque doit diminuer avec la taille du groupe. B. Le risque doit diminuer avec la vigilance. C. Le vigilance doit avoir un coût, en terme d'acquisition des ressources par exemple. De D à F on compare deux individus, un qui diminue sa vigilance avec l'augmentation de la taille de groupe (D, ligne verte pointillée) et l'autre qui ne change pas de comportement (D, ligne bleue pleine). L'individu qui diminue sa vigilance augmente son acquisition des ressources (E), mais fait aussi face à un risque de prédation plus élevé que l'individu qui ne change pas de comportement (F). La diminution de la vigilance avec la taille de groupe sera une stratégie viable si les bénéfices (1) sont supérieurs aux coûts (2). Ce raisonnement peut s'appliquer avec d'autres comportements anti-prédateur, à la place de la vigilance, par exemple l'utilisation de l'espace.

solitaire. Murthy et al. (2016) suggèrent aussi qu'il peut exister des contraintes aux déplacements collectifs incompatibles avec une utilisation efficace des milieux risqués. En effet, maintenir la cohésion du groupe implique souvent de maintenir des distances inter-individuelles relativement faibles et de s'orienter en fonction de ses voisins (Ballerini et al. 2008; Bode et al. 2010; Ioannou et al. 2012). D'un autre côté, pour gérer le compromis entre acquisition de ressources et risque de prédations dans un milieu risqué, un individu peut bénéficier de déplacements plus grands et moins prévisibles (Fortin et al. 2009), ce qui peut diminuer la cohésion. L'étude de Murthy et al. (2016) regarde cependant les conséquences du grégarisme sur une courte échelle temporelle et sans conséquences réelles en terme d'acquisition des ressources ni d'évitement de la prédation. Ces deux expériences analysent l'ajustement au risque perçu par rapport à un habitat, sans aucun indice de présence de prédateur ni aucune acquisition de ressource. Les individus solitaires utilisent d'ailleurs de plus en plus les milieux risqués au fur et à mesure de l'expérience, ce qui pourrait s'expliquer par le fait qu'ils identifient l'absence de risque immédiat (Murthy et al. 2016).

Chez les bisons des prairies (*Bison bison bison*), (Fortin et al. 2009) ont néanmoins montré que la sélection de l'habitat changeait en fonction de la taille du groupe et notamment que les grands groupes sélectionnaient plus fortement les milieux risqués. Les liens entre la taille de groupe et l'habitat chez les ongulés sont rendus plus compliqués par les dynamiques de fusion-fission qu'on y observe fréquemment (Aureli et al. 2008). En effet l'habitat peut influer fortement sur ces dynamiques en changeant les taux de fusion et de fission, notamment par la plus grande visibilité dans les milieux ouverts. On peut alors observer des groupes de tailles plus importantes dans les milieux ouverts, non pas parce qu'il y a eu une diminution d'investissement anti-prédateurs (évitement des milieux ouverts risqués) mais simplement parce que la visibilité accrue augmente les chances de fusion de groupes et donc conduit à une taille de groupe plus importante (Gerard and Loisel 1995; Pays et al. 2007). Fortin et al. (2009) utilisent cependant une fonction de sélection de ressources (Johnson et al. 2004; Boyce 2006) dont les coefficients de sélection dépendent de la taille du groupe. Ils ne montrent donc pas que les groupes sont de taille plus importante en milieu risqué, mais que les grands groupes sélectionnent davantage les milieux risqués que les petits groupes. Ils montrent aussi que cette différence provient d'un temps de résidence plus important dans les prairies, ce qui invalide l'hypothèse alternative de la compétition pour la ressource accrue dans les groupes, laquelle mènerait vers des temps de résidence plus faibles du fait de l'exploitation des ressources plus importante.

Si les études de l'effet de la taille de groupe sur l'utilisation de l'espace ne sont pas plus répandues, c'est probablement lié à la difficulté de suivre à la fois ces deux aspects. Les groupes peuvent être extrêmement dynamiques et pour ne pas subir des effets confondants comme les changements de dynamique de fusion-fission (Gerard and Loisel 1995; Pays et al. 2007) il faut nécessairement des groupes suffisamment stables pour qu'on puisse suivre leur utilisation de l'espace sur une durée plus longue et en déduire des ajustements à long terme des investissements anti-prédateurs. Les analyses complémentaires du Chapitre 1 montrent un exemple de ce type. Les groupes de zèbres étant stables dans le temps, sur plusieurs années (Rubenstein 1986), ils offrent une occasion idéale de vérifier si les différences de taille de groupe à long terme offrent l'opportunité de diminuer les investissements anti-prédateurs et d'utiliser ainsi des endroits plus risqués du paysages. Si les résultats ne sont pas complètement fiables du fait de la taille d'échantillonnage limitée, ils suggèrent cependant une validation de cette dernière hypothèse.

Course spatiale et migrations quotidiennes

Prédateurs et proies sont entraînés dans une course spatiale (Sih 1998, 2005) dans laquelle ils ont des intérêts divergents, leur recouvrement spatial étant avantageux pour le prédateur mais pas pour la proie. Sih (2005) prévoit que le recouvrement spatial dépend des ancres spatiales du prédateur et de la proie, plus précisément du joueur qui subit les contraintes spatiales les plus importantes - les ancres ou contraintes spatiales étant des caractéristiques du paysage ayant des conséquences pour le prédateur ou la proie (vulnérabilité hétérogène, répartition des ressources de la proie, présence d'une tanière, d'un terrier, d'un territoire ...). De nombreuses études ont examiné cette course spatiale

et comparé l'utilisation de l'espace par les prédateurs et par leur proies, en tenant compte des ressources des proies et de l'habitat, afin de mieux cerner les potentielles ancres spatiales (Hammond et al. 2007; Fauchald 2009; Thaker et al. 2011; Arias-Del Razo et al. 2012; Courbin et al. 2014). On sait par ailleurs que prédateurs et proies sont entraînés dans une course temporelle dans laquelle ils ont des intérêts divergents face au recouvrement de leur rythme d'activité (Arias-Del Razo et al. 2011; Monterroso et al. 2013). La résolution de cette course temporelle peut aussi reposer sur les contraintes du prédateur et de la proie. Par exemple, le taux de succès des attaques d'un prédateur peut être supérieur la nuit (Hayward and Slotow 2009), ce qui contraint alors fortement son utilisation du temps, il a moins d'intérêt à tenter de chasser la journée. On s'attend à ce qu'il perde la course temporelle et que le recouvrement temporel avec les proies soit limité. Prédateurs et proies n'ajustent pas leur seule utilisation de l'espace ou bien leur rythme d'activité en réaction à l'autre joueur, mais potentiellement les deux, ainsi que d'autres comportements encore. Les réactions spatio-temporelles au risque de prédation sont bien connues en milieu aquatique (Alonzo et al. 2003; Hays 2003; Benoit-Bird and Au 2006; Sainmont et al. 2013), mais elles ont été relativement peu décrites en milieu terrestre, si ce n'est en rapport avec les activités humaines (Tolon et al. 2009; Fortin et al. 2015). Dans le Chapitre 2, je décris un tel phénomène, entre les zèbres et les lions. On peut réinterpréter cet exemple dans le cadre d'une course comportementale (Sih 1984). Les zèbres sont contraints par la distribution de leurs ressources, concentrées autour des points d'eaux dans des grandes zones ouvertes. Les lions sont contraints par la distribution de leurs proies, globalement concentrées à proximité des points d'eaux (Valeix et al. 2009) et par leur efficacité de capture, souvent supérieure la nuit (Elliott et al. 1977; Van Orsdol 1984). Ainsi si l'on ne prend pas en compte l'existence du cycle circadien et plus particulièrement du rythme d'activité du prédateur, on peut penser que les zèbres n'ont pas ou peu de réactions au risque de prédation et en particulier qu'ils perdent la course spatiale (Sih 2005), c'est à dire que l'utilisation de l'espace du prédateur et celui de la proie se recouvrent fortement si l'on prend l'ensemble de la journée. C'est ce que concluait Valeix et al. (2009) en se basant sur des comptages diurnes de proies. À l'inverse, si on sépare le jour et la nuit, on se rend compte que le recouvrement est fort la journée, pendant les moments d'inactivité et donc de plus faible risque de la part du prédateur, et plus faible la nuit, pendant les moments d'activité du prédateur. La course spatiale est de ce point de vue plus favorable aux proies qu'au prédateur.

Les processus de recherche et d'évitement des prédateurs et proies

Comme on l'a vu précédemment, l'utilisation de l'espace intervient à plusieurs étapes de la séquence de prédation, lors des étapes de rencontre, de détection et d'attaque (étapes 1, 2 et 4, fig.1 de l'introduction). De nombreuses études ont montré son importance à travers l'effet de l'habitat sur l'interaction prédateur-proie. De manière directe, l'habitat change la probabilité de détection de la proie par le prédateur ainsi que le taux de

succès des attaques à travers la probabilité de détection du prédateur par la proie (Kunkel and Pletscher 2000; Thogmartin and Schaeffer 2000), selon qu'il présente plus ou moins de refuges (Koivunen et al. 1998; Friedlander and Parrish 1998). De manière indirecte, l'habitat structure aussi la probabilité de rencontre du prédateur et de la proie. En effet, les probabilités de rencontre sont déterminées par l'utilisation conjointe de l'espace par le prédateur et la proie, et cette utilisation dépend fréquemment des habitats (Courbin et al. 2009 ; Chapitre 2 ; Viejou et al. 2018). L'utilisation de l'espace du prédateur et de la proie n'est cependant pas complètement déterminée par l'habitat. On observe en effet des variations importantes de temps de résidence et de retour dans les parcelles d'un même habitat (Laundré 2010; Courbin et al. 2014) et de nombreux autres facteurs peuvent structurer l'utilisation de l'espace (approvisionnement à un lieu central, Pinaud and Weimerskirch 2005 ; territoires, Rubenstein 1986, Bekoff and Wells 1982 ; tanières, Mauritzen et al. 2001).

Dans cette thèse, on trouve deux exemples de processus où la probabilité de rencontre entre prédateur et proie n'est pas complètement décidée par la sélection de l'habitat. Le Chapitre 2 montre un cas de figure où la proie s'éloigne quotidiennement des zones fortement utilisées par le prédateur, pendant la période la plus risquée de la journée. Contrairement aux migrations quotidiennes que l'on connaît en milieu aquatique (Hays 2003; Sainmont et al. 2013), cette réaction n'est pas ici déclenchée par des différences de caractéristiques des habitats (quantité de ressources, vulnérabilité variable dans le temps ou l'espace ...) mais bien directement par l'utilisation de l'espace et le rythme d'activité du prédateur. Le Chapitre 3 présente quant à lui un modèle de sélection de parcelle où les prédateurs et les proies peuvent se déplacer en fonction de leur mémoire des rencontres prédateur-proie passées et de leur estimation de la ressource des proies dans les différentes parcelles. L'investigation des stratégies optimales du prédateur et de la proie à travers de nombreux environnements montre l'importance potentielle de l'imprévisibilité du déplacement, les prédateurs ayant parfois intérêt à ignorer leurs connaissances des parcelles pour se déplacer aléatoirement et rendre moins efficace l'évitement par les proies des zones de rencontre.

Cette idée de jeu de passe-passe a été proposée par Mitchell and Lima (2002) : elle montrait à l'origine que les proies pouvaient diminuer leur probabilité de rencontre en se déplaçant aléatoirement entre les parcelles de leur domaine vital. L'efficacité de cette stratégie était cependant fortement dépendante de la mémoire spatiale des prédateurs (Mitchell and Lima 2002; Mitchell 2009). Ici on a développé un modèle où les proies aussi pouvaient utiliser leur mémoire des rencontres passées et l'ensemble des environnements testés montraient au contraire l'importance pour les prédateurs d'être imprévisibles. Cette différence peut s'expliquer si l'on détaille les coûts et bénéfices d'un déplacement aléatoire et donc imprévisible pour les prédateurs et les proies. Pour les proies, il y a deux coûts. D'abord les proies peuvent utiliser des parcelles où le risque de prédation est plus important et qui seraient potentiellement évitées si le déplacement prenait en compte cette information. En se déplaçant aléatoirement, les proies pâtissent aussi d'une exploitation moindre des parcelles ayant davantage de fourrage. Ce dernier coût est probablement plus important dans notre modèle du fait de la prise en compte de la déplé-

tion et de la compétition avec les autres proies, ces mécanismes n'étant pas inclus dans les précédents modèles du jeu de passe-passe (Mitchell and Lima 2002; Mitchell 2009). Les prédateurs, par contre, risquent simplement d'utiliser des parcelles où les proies ne sont pas très présentes ou peu vulnérables. Les bénéfices sont relativement similaires : l'imprévisibilité empêche le prédateur ou la proie d'ajuster efficacement son utilisation de l'espace. Les résultats du modèle suggèrent ainsi que les coûts sont plus importants pour la proie que pour le prédateur et on s'attend donc à ce que les proies soient plus prévisibles que leurs prédateurs, une prévision à même d'être testée.

Le jeu de passe-passe est donc un exemple de processus qui influe les probabilités de rencontre indépendamment de l'habitat : c'est la dynamique du déplacement qui est importante. Ces questions ont donné lieu à un nombre limité d'études empiriques (Gude et al. 2006; Fortin et al. 2009; Laundré 2010). Gude et al. (2006) ont montré que la probabilité de présence des wapitis dans les zones cœurs de l'aire de chasse des loups après le départ de ces derniers diminue fortement en quelques jours. Étant donné la très bonne mémoire spatiale des loups, cette réaction était interprétée comme la nécessité pour les wapitis d'être imprévisibles. Un tel patron rappelle les réponses réactives des zèbres qui, après une rencontre avec les lions, s'éloignent de 4 à 5 kilomètres en 24 à 48h (Courbin et al. 2016). Cette réaction pourrait, elle aussi, être interprétée dans le cadre d'un jeu de passe-passe comme la nécessité d'être imprévisible pour la proie. Étant donné que le risque qui contraint ces deux réactions est immédiat et pas uniquement futur, il reste cependant difficile de différencier l'importance de l'imprévisibilité des proies de celle de la fuite d'un risque immédiat, particulièrement grave dans le cas des lions, prédateurs à l'affut. Chez les bisons, (Fortin et al. 2009) ont établi que les petits groupes quittaient les prairies, habitat risqué et riche en ressources, plus précocement que les grands groupes. Ce résultat est contraire à l'interprétation d'une utilisation de l'espace dirigée par la compétition pour les ressources, où les grands groupes devraient épuiser avant les plus petits les ressources d'une prairie. Dans le cadre d'un jeu de passe-passe cependant, les bisons ont intérêt à se déplacer de manière imprévisible et donc relativement fréquemment. Dans ce cas les petits groupes, plus à risque que les grands, seraient contraints à des mouvements plus fréquents et imprévisibles.

L'étude du jeu de passe-passe et sa prise en compte dans les interactions proie-prédateur nécessite ainsi une approche comportementale à l'échelle du paysage (Lima and Zollner 1996) prenant en compte l'importance de la mémoire spatiale des prédateurs et proies (Wolf et al. 2009; Oliveira-Santos et al. 2016; Merkle et al. 2017; Bracis et al. 2015, 2018). Le modèle du Chapitre 3, s'inscrit dans ce cadre et propose un moyen d'évaluer l'importance relative de deux types de mémoire, de travail et de référence (Bailey et al. 1996), des rencontres prédateurs-proies passées et de la ressource des proies dans l'estimation de l'intérêt d'une parcelle pour les prédateurs et les proies. Ces travaux soulignent ainsi l'importance des processus d'évitement basés sur la dynamique du déplacement plutôt que sur les déplacement orientés en fonction des préférences d'habitat. Si les réactions spatiales des proies aux déplacements des prédateurs commencent à être connues (Fortin et al. 2009; Courbin et al. 2016, Chapitre 2), l'étude des comportements de prospection des prédateurs concerne généralement des proies immobiles ou dénuées

de réactions comportementales (e.g. Benhamou 2007). Conceptuellement cependant, la théorie de la recherche ('search theory') étudie l'efficacité des stratégies de recherche spatiale (Zoroa et al. 2011, 2015; Gal et al. 2015; Ross and Winterhalder 2015; Hohzaki 2016). Ces travaux se basent fortement sur la théorie des jeux, ce qui permet de prendre en compte les réactions réciproques des prédateurs et des proies ((Lima 2002). Actuellement ces travaux ont cependant peu de liens avec des observations empiriques de systèmes prédateurs-proie.

Stratégies optimales et modèles théoriques dans le jeu prédateur-proie

Dans cette thèse nous avons utilisé des approches empiriques (Chapitre 2) et théoriques (Chapitres 1 et 3), sans pour autant les relier directement. Si l'idéal est généralement de pouvoir comparer les prévisions d'un modèle théorique avec des observations empiriques (par ex. (Goss-Custard and Stillman 2008; Bennett et al. 2009; Fortin et al. 2015), une telle approche n'est pas toujours possible, que les limites soient liées aux difficultés techniques d'acquisition de données ou à la complexité trop importante des modèles les rendant difficiles à paramétrer. Ainsi pour pouvoir tester les prévisions du modèle du Chapitre 1, ou une modification du modèle, il faudrait pouvoir caractériser les différentes parcelles disponibles et leurs bénéfices associés ainsi que l'estimation du risque de prédation et pouvoir suivre simultanément l'utilisation de l'espace et la vigilance des individus, ce qui est techniquement encore compliqué même si les capteurs d'activité que l'on peut associer aux colliers GPS pourraient permettre de lever ces limitations (Roberts et al. 2016). Une fois paramétrés avec des données empiriques, les modèles théoriques peuvent éclairer certaines situations, par exemple en spécifiant les contraintes durant l'approvisionnement d'un individu, comme la nécessité de maximiser l'énergie acquise ou la prise en compte d'un ratio entre l'énergie et le risque de prédation (Fortin et al. 2015). Cependant les modèles théoriques peuvent aussi permettre de proposer des idées et de développer des concepts à même d'éclairer des observations empiriques : le modèle du jeu de passe-passe de Mitchell and Lima (2002), même s'il représente des situations simplifiées et incomparables avec un système prédateur-proie réel, a permis de développer et de promouvoir l'importance de la mémoire et donc de l'imprévisibilité des déplacements dans le jeu spatial proie-prédateur. Même si on ne peut directement et précisément comparer les prévisions du modèle avec des données empiriques, ce modèle peut apporter un éclairage sur certains patrons comme les déplacements fréquents parfois observés chez les ongulés (Fortin et al. 2009).

En ce sens, les deux modèles proposés dans les Chapitres 1 et 3 complètent les théories existantes pour les comportements anti-prédateurs et le jeu spatial prédateur-proie. Le modèle du Chapitre 1 souligne l'importance de l'utilisation de l'espace et de son interaction potentielle avec la taille de groupe et la vigilance : il pourrait expliquer la complexité des liens observés entre la vigilance et la taille de groupe chez les espèces sociales comme les primates et les équidés (Treves 2000; Burger and Gochfeld 1994; Creel et al. 2014). Le

modèle du Chapitre 3 quant à lui développe l'idée du jeu de passe-passe de Mitchell and Lima (2002) pour le cas où prédateur et proie peuvent utiliser leur mémoire pour tenter de mieux réagir aux comportements spatiaux de l'autre joueur et à la répartition du fourrage des proies. Il permet aussi de proposer un cadre pour mesurer l'intérêt de l'information passée dans les choix de parcelles des prédateurs et des proies. Des études empiriques de sélection d'habitat suggèrent justement le rôle effectif de la mémoire lors des déplacements (Wolf et al. 2009; Oliveira-Santos et al. 2016) mais ne peuvent déterminer s'il est intéressant pour les proies ou les prédateurs de se servir de ces informations, ni préciser quelle en serait l'utilisation optimale.

C'est là la force des méthodes de programmation dynamique (Mangel and Clark 1986; Houston et al. 1988) et d'algorithme génétique (Hamblin 2013; Sirot et al. 2016) utilisées respectivement dans les Chapitres 1 et 3. Dans un modèle, il est facile de montrer qu'un comportement est plus adaptatif qu'un autre et d'en déduire l'importance d'un mécanisme (Bracis et al. 2015, 2018; Riotte-Lambert et al. 2015). Pour autant, les alternatives comportementales dans les modèles sont parfois très nombreuses, et on n'a alors aucune idée de la réussite effective des quelques comportements sélectionnés par rapport à l'ensemble des alternatives. Lorsqu'une stratégie optimale par rapport aux règles fixées dans le modèle est obtenue, on a un point de comparaison objectif des stratégies. Cependant, on ne s'attend pas forcément à retrouver ces comportements optimaux dans les études empiriques, du fait notamment des simplifications du modèle, des hypothèses à vérifier ou des limitations des capacités cognitives, physiologiques ou morphologiques qui ne permettraient pas ce comportement. La comparaison avec un comportement optimal issu d'un modèle permet néanmoins de se situer objectivement par rapport aux contraintes que l'on a identifiées.

Conclusion

Finalement, au cours de cette thèse, j'ai contribué à améliorer la compréhension du jeu spatial entre prédateur et proie. Ce jeu spatial doit prendre en compte de manière intégrative l'ensemble des options comportementales disponibles pour les deux joueurs (Chapitres 1 et 2). Il doit aussi considérer que les décisions spatiales d'un joueur vont fortement dépendre des décisions spatiales des autres joueurs (Chapitres 2 et 3), ce qui induit de prendre en compte simultanément les réactions comportementales des prédateurs et des proies (Lima 2002), et souligne aussi l'importance de considérer la dynamique du déplacement dans le calcul des probabilités de rencontre entre prédateurs et proies (Chapitre 3). Dans cette thèse, j'ai finalement apporté des développement au concept d'écologie comportementale du paysage (Lima and Zollner 1996) en proposant un modèle théorique permettant de prévoir comment l'information acquise par un individu peut être utilisée pour sélectionner une parcelle dans le cadre d'un jeu prédateur-proie.

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Spatial game and behavioural interaction in the predator-prey interaction

Predators and prey engage into a space race where predators seek to select areas with high prey availability while prey try to avoid areas with a high probability of encountering a predator. Predators and prey continuously make choices that can alter the outcome of this space race. For example, by using different locations in the landscape, they can alter the probability of an encounter, the probabilities of detection or the probability of success of an attack. Many empirical studies show the importance of habitat in these choices. On the other hand, little is known about avoidance by prey or predator search strategies that would be unrelated to habitat. The space race, however, does not fully summarize the interaction between predators and prey, which also depends on many non-spatial behaviors. The vigilance and grouping behaviour of prey are relatively common defenses, and there are many examples where prey become active at another time of day to escape their predator. However, it is still unclear how those behaviors interact with the spatial dimension of the prey-predator game. In this thesis, I will try to fill these gaps. In the first chapter, I propose a theoretical model showing the importance of accounting for spatial behaviors when studying the classical interaction between vigilance and group size in prey. In the second chapter, I present a mechanism of predator avoidance by prey, relying on the spatial and temporal anchors of predators and independent on the habitat. Finally, in the last chapter, I develop a patch selection model to predict how past information should be used to determine movement. This model emphasize the importance of movement unpredictability in the predator-prey game. These different works are part of a behavioral ecology of the landscape and aim to integrate behavioral mechanisms in the study of ecological dynamics at the landscape scale.

Jeu spatial et interactions comportementales dans l'interaction prédateur-proie

Prédateurs et proies sont entraînés dans une course spatiale où les prédateurs cherchent à sélectionner les zones du paysage avec une forte disponibilité en proies alors que les proies tentent d'éviter les zones du paysage avec une forte probabilité de rencontrer un prédateur. Ils procèdent incessamment à de nombreux choix susceptibles de modifier l'issue de cette course. Ainsi, en sélectionnant des endroits différents, ils peuvent tenter d'altérer les probabilités de détection, de rencontre ou encore la probabilité de réussite d'une attaque. De nombreuses études empiriques montrent l'importance de l'habitat dans ces choix. On connaît par contre peu les mécanismes de recherche (par les prédateurs) ou d'évitement (par les proies) qui ne seraient pas relatifs à l'habitat. La course spatiale ne résume cependant pas entièrement l'interaction entre prédateurs et proies, laquelle dépend de nombreux comportements non-spatiaux. La vigilance et la socialité des proies constituent des défenses relativement répandues. On a aussi fréquemment observé de nombreux exemples où les proies deviennent actives à un autre moment de la journée pour échapper à leur prédateur. Cependant, on connaît relativement peu les interactions de ces comportements avec la dimension spatiale du jeu proie-prédateur. Dans cette thèse, j'ai pour objectif de combler ces différents manques. Dans le premier chapitre, je propose un modèle théorique montrant l'importance de la prise en compte des comportements spatiaux dans l'interaction classique entre vigilance et taille de groupe chez les proies. Dans le second chapitre, je présente un mécanisme d'évitement des prédateurs par les proies, s'appuyant sur les ancres spatiales et temporelles des prédateurs et ne dépendant pas de l'habitat. Enfin, dans le dernier chapitre, je développe un modèle de choix de parcelles permettant de prévoir comment les connaissances passées sont susceptibles d'être utilisées pour orienter les déplacements. Ce modèle rappelle notamment l'importance de l'imprévisibilité du déplacement dans le jeu prédateur-proie. Ces différents travaux se placent dans le cadre d'une écologie comportementale du paysage et visent à intégrer des mécanismes comportementaux dans l'étude des dynamiques écologiques à l'échelle du paysage.