



**HAL**  
open science

# CHANGEMENT GLOBAL ET DYNAMIQUE DE SELECTION D'HABITAT DE REPRODUCTION D'UN OISEAU NICHANT AU SOL CAS DU BUSARD CENDRE EN MILIEU AGRICOLE INTENSIF

Hanneke Gillis

► **To cite this version:**

Hanneke Gillis. CHANGEMENT GLOBAL ET DYNAMIQUE DE SELECTION D'HABITAT DE REPRODUCTION D'UN OISEAU NICHANT AU SOL CAS DU BUSARD CENDRE EN MILIEU AGRICOLE INTENSIF. Sciences de l'environnement. Université Pierre et Marie Curie - Paris VI, 2011. Français. NNT: . tel-00660268

**HAL Id: tel-00660268**

**<https://theses.hal.science/tel-00660268>**

Submitted on 17 Jan 2012

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

**THESE DE DOCTORAT DE  
L'UNIVERSITE PIERRE ET MARIE CURIE**

Spécialité Ecologie  
Ecole Doctorale Diversité du Vivant

Présentée par  
**M<sup>lle</sup> Hanneke GILLIS**

Pour obtenir le grade de  
**DOCTEUR de l'UNIVERSITÉ PIERRE ET MARIE CURIE**

soutenue le 22 novembre 2011 à 9h  
au laboratoire du CNRS de Chizé

---

**CHANGEMENT GLOBAL ET DYNAMIQUE DE SELECTION D'HABITAT  
DE REPRODUCTION D'UN OISEAU NICHANT AU SOL**

CAS DU BUSARD CENDRE EN MILIEU AGRICOLE INTENSIF

---

Devant le jury composé de :

M. Jean-Louis MARTIN, Directeur de recherche (HDR), CEFÉ-CNRS	Rapporteur
M. Jean SECONDI, Maître de conférences (HDR), Université d'Angers	Rapporteur
M. Luc BARBARO, Chargé de recherche, INRA Cestas	Examineur
M. François SARRAZIN, Professeur, Université Pierre et Marie Curie	Examineur
M. Vincent BRETIGNOLLE, Directeur de recherche, CNRS	Directeur de thèse



*A ma famille...*

*A Ramzi...*



Alexis Nouailhat



## Remerciements

Ça y est, voici le moment des remerciements...en espérant n'oublier personne...

Tout d'abord merci aux rapporteurs : Jean Secondi et Jean-Louis Martin ainsi qu'aux examinateurs, Luc Barbaro et François Sarrazin, d'avoir accepté d'évaluer cette thèse.

Merci à l'Ecole Doctorale Diversité du Vivant pour le financement de cette thèse, plus particulièrement à Hervé Le Guyader et à la chaleureuse et toujours disponible Marie Donatien mais aussi à Gaëlle Boutin qui lui a succédé.

Merci à Vincent Bretagnolle de m'avoir offert l'opportunité de réaliser cette thèse et de m'avoir accompagné durant ces 3 années. Merci également pour les soirées dégustations œnologiques accompagnées de bonne musique jamaïcaine.

Merci à Martine Guérif, Marie Weiss, Sergio Castillo et Alexandre Millon pour les fructueuses collaborations.

Merci à toute l'équipe AgriPop et en particulier à Bertrand (pour ton aide, ton soutien, tes conseils et pour nos discussions enrichissantes professionnellement ou non) mais aussi à Isabelle, Sylvie et Patrick.

Merci aux relecteurs de dernière minute : Bertrand, Isabelle, Vincent L., Florian, Sabrina, JB et Paul M.

Merci à tous ceux ayant contribué à la récolte des données pendant et avant ma thèse.

Merci à Rémi, stagiaire le temps d'une saison, pour les moments partagés sur le terrain (c'était quand même bien de chercher des faux œufs dans du blé à 1h du mat' !), pour sa façon simple et discrète de vivre sa passion pour la nature...

Un grand Merci à tout le personnel du laboratoire qui a contribué de près ou de loin à ce projet :

Merci à Delphine (oui ma petite !) et Evelyse pour leur bonne humeur et leur disponibilité.

Merci aussi à Christophe, notre charismatique mais non moins talentueux cuistot, mais aussi à Micheline et son successeur Arnaud : les pauses déjeuner ont toujours été des grands moments de plaisir !

Merci également à JJ, André, Simon, Patrice, Xavier D., Xavier B., Noel & Nadine, Marylin, Edo & David.

Merci aux membres du CAES pour les fêtes de Noël et d'été : mémorables !

Merci aux collègues de poterie : Karine, Hélène, Zézèlle, Sophie, Marie ; un peu de travail manuel ne peut pas faire de mal !

Pour avoir contribué à mon bien être tout au long de cette thèse, merci aux étudiants du labo, les anciens, actuels et futurs :

Les premiers pour m'avoir accompagné durant mes premiers pas à Chizé, notamment Alex, Jess, Léo, Audrey Blondi, Oliv, Marie R., Fred QuaterBack, Catherine (Fo pâ gâché !), Jim, Clara, Aurélie G., Roger, Benoit, Victor, Vincent Lecomte...

Les seconds pour m'avoir soutenu et encouragé mais aussi pour m'avoir sorti la tête du guidon quand c'était nécessaire : merci donc à Steve, Matthieu A., JF, Damien, Anne-Cécile, Hélène G., Miches, Stefaniya, Sophie, Paul M., Débi, Thibaut, Fabrice, Morgane, Max, Zézèlle, Helmut, Luca (merci pour le titre !) et un spécial GRAND merci :

- aux membres du Clan Chuck Paradise : Hélène L (merci pour les photos des pages de transitions), Adrien Roberto (Anne-Marie Katrien est fier de nous, j'en suis sûre), Vincent L (un jour, on ira au Mexique !) et Flo (non tu ne travailles pas sur les méga-herbivores) mais aussi Thomas (et sa petite cuillère)

- à la bande de Secondigné : Mathieu L (entre fils et fille de, on se comprend), Jade (pour ses phrases mythiques et mystiques), Aurélie (é Cend'é ! é San Mat'in !) et Kévin (pour ton soutien et ton aide dans le travail mais aussi pour ta joie de vivre et pour les papillons discrets).

- à ma toujours « rayonnante » coloc' : Sabrinette mais aussi à JB, pour m'avoir soutenu durant les difficiles derniers mois. Merci d'avoir supporté mes long discours plaintifs et merci pour les bonnes petites assiettes qui m'attendaient parfois le soir !

- à Anne-Marie Katrien ...

Merci également à mes amis Limougeauds : Nizar, Mag, Pascal et So pour leur soutien et pour les moments de retrouvailles, peu fréquents, certes, mais toujours ravigotants ! Ne lâchons rien, continuons !

Je ne remerciais jamais assez ma famille : mes parents, Loe & Hilde, pour avoir financé une bonne partie de mes études mais aussi et surtout pour leur soutien moral et les encouragements constants. J'y suis arrivée ! Merci de m'avoir poussé à aller toujours plus loin. Merci également à Fem et Marie, mes sœurs adorées, pour leur présence et soutien. Merci à mon frère, Jelle, qui suit ça de loin mais qui suit. Merci aussi aux petits loups, Pierre et Juliette.

Enfin merci à ma moitié, Ramzi, qui a toujours été là durant cette thèse, mais aussi durant les années précédentes, dans les bons moments comme dans les difficiles. Merci pour ton écoute et ton réconfort (« ça va bien aller ! »)... même à distance. Une page de notre vie se tourne avec la fin de cette thèse mais j'attends la suite avec impatience...





# Communications & articles

## *Articles présentés dans la thèse*

Bretagnolle, V. & Gillis, H. Predator-prey interactions and climate change. *Effects of Climate Change on Birds, Oxford Univ Pr*, 2010, 227-248.

**Gillis H.**, Gauffre B., Huot R. & Bretagnolle V. Vegetation height and egg coloration differentially affect predation rate and overheating risk: an experimental test mimicking a ground-nesting bird. **Soumis à Canadian Journal of Zoology**

**Gillis H.**, Millon A. & Bretagnolle V. 2011. Where and when to breed do matter: temporal variation in selection of vegetation height at the nest for a ground-nesting raptor in farming habitats. **Soumis à Oikos**

**Gillis H.** & Bretagnolle V. 2011. Is there a balance between physical and social cues for nesting habitat choice in a facultative colonial breeder? **En préparation.**

**Gillis H.**, Le Rest K., Guérif M., Castillo S., Weiss M. and Bretagnolle V. Breeding habitat selection of a farmland ground-nesting bird: an approach at multiple spatio-temporal scales using remote sensing. **En préparation**

## *Communications*

**Gillis H.**, Gauffre B., Huot R., & Bretagnolle V. « Vegetation height and egg coloration differentially affect predation rate and overheating risk: an experimental test mimicking a ground-nesting bird. **Présentation orale** – 7èmes rencontres « Ecology & Behaviour »: Rennes, 2-6 mai 2011.

**Gillis H.** « Changement global –habitat – succès de reproduction. Cas du Busard cendré *Circus pygargus* en milieu agricole intensif ». **Présentation orale** – Réunion Programme ANR BiodivAgrim: Chizé, 6-7 déc. 2010.

**Gillis H.** « Vegetation height and nest-site selection in a ground-nesting bird in a intensive agricultural habitat ». **Poster** – Edward Grey Institute Conference: Oxford, 7-9 janv. 2010

**Gillis H.** « Impact du changement global sur un rapace prédateur spécialiste nichant en milieu agricole intensif ». **Présentation orale** – Réunion Programme ANR BiodivAgrim: Rennes, 7-8 déc. 2009.

**Gillis H.** & Bretagnolle. « Pourquoi les busards cendrés établissent-ils leurs nids à partir d'une certaine hauteur de végétation? ». **Présentation orale** – 16ème rencontre du réseau busards: Chizé, 27-29 nov. 2009.

**Gillis H.** & Bretagnolle V. « Impact of climate change on a predator-prey relationship in a raptor species ». **Présentation orale** – 2nd European Congress of Conservation Biology: Prague, 1-5 sept. 2009.

**Gillis H.** « Relation habitat de reproduction/succès de reproduction: Impact des changements globaux ». **Présentation orale** – Réunion Programme ANR BiodivAgrim: Toulouse, 24-25 nov. 2008.



# Sommaire

<b>A. Introduction</b> .....	<b>1</b>
<b>A.I. Changement global et réponses des organismes</b> .....	<b>2</b>
A.I.1. Définition du changement global .....	2
A.I.2. Réponses des organismes au changement global .....	5
A.I.2.i. Effets directs .....	6
A.I.2.ii. Effets indirects à travers l'habitat .....	8
A.I.2.ii.a. Définition d'un habitat .....	8
A.I.2.ii.b. Réponses des organismes au changement global à travers l'habitat .....	11
• Effets indirects à travers l'habitat physique .....	11
• Effets indirects à travers l'habitat biologique .....	12
• Effets indirects à travers l'habitat social .....	37
<b>A.II. Des milieux particulièrement soumis au changement global : Les espaces agricoles</b> ..	<b>39</b>
A.II.1. Généralités .....	39
A.II.2. Zone d'étude : Zone Atelier Plaine et Val de Sèvre .....	42
<b>A.III. Un taxon particulier : Les oiseaux</b> .....	<b>44</b>
A.III.1. Les oiseaux : un taxon largement étudié mais approprié .....	44
A.III.2. Modèle biologique d'étude : Le Busard Cendré <i>Circus pygargus</i> .....	46
<b>A.IV. Objectifs et structure de la thèse</b> .....	<b>53</b>
<b>B. Principaux résultats</b> .....	<b>57</b>
<b>B.I. processus sous-jacents à la sélection d'un site de nidification chez le busard cendré</b> ..	<b>59</b>
B.I.1. Résumé du chapitre .....	59
B.I.2. Article 1 .....	63
<b>B.II. Variation temporelle des patrons de sélection du site de nidification du Busard cendré : Influence des composantes de l'habitat</b> .....	<b>80</b>
B.II.1. Résumé du chapitre .....	80
B.II.2. Article 2 .....	84
<b>B.III. Patrons temporels d'installation dans une colonie : l'importance des voisins</b> .....	<b>102</b>
B.III.1. Résumé du chapitre .....	102
B.III.2. article 3 .....	105
<b>B.IV. Etude de la sélection d'habitat à différentes échelles spatio-temporelles</b> .....	<b>122</b>
B.IV.1. résumé du chapitre .....	122
B.IV.2. Article 4 .....	126
<b>C. Synthèse générale, discussion et perspectives</b> .....	<b>145</b>
<b>C.I. Principaux résultats obtenus</b> .....	<b>146</b>
<b>C.II. Quel avenir pour le Busard cendré dans le contexte du changement global?</b> .....	<b>148</b>
C.II.1. Si les tendances se confirment .....	148
C.II.2. Le changement global, cause des variations temporelles observées ? .....	152
C.II.3. Une prochaine étape : Modéliser pour prédire .....	154
<b>C.III. Conservation du Busard cendré en milieu agricole dans le contexte du changement climatique</b> .....	<b>156</b>
C.III.1. Mesures de conservation actuelles et efficacité face au changement global .....	156
C.III.1.i. Un dispositif de protection des nids .....	156
C.III.1.ii. Une Zone de Protection Spéciale .....	157
C.III.2. Propositions de mesures pérennes adaptées au changement global: .....	158
C.III.2.i. Favoriser la colonisation des milieux naturels .....	159
C.III.2.ii. Création d'un habitat idéal et Mise en place d'une MAE ? .....	160
<b>D. Références bibliographiques</b> .....	<b>163</b>



# A. Introduction



## **A.I. CHANGEMENT GLOBAL ET REPOSES DES ORGANISMES**

### **A.I.1. Définition du changement global**

L'histoire de la vie sur terre témoigne de cinq vagues d'extinctions de masse des espèces, résultats d'évènements naturels. D'après de nombreux spécialistes, il est maintenant admis qu'une sixième vague d'extinction est en cours sous l'effet du changement global qui recouvre des changements à la fois climatiques et environnementaux, résultats de l'action humaine. L'impact des changements abiotiques et biotiques de l'environnement sur les réactions et les adaptations des plantes et des animaux a toujours été une question centrale en biologie évolutive (Møller et al. 2010), mais le contexte du changement global apporte une dimension supplémentaire à cette question. Ainsi, un des objectifs majeurs de l'écologie actuelle est de déterminer comment le changement global récent affecte les populations et les écosystèmes afin de prédire et de limiter les conséquences de ces changements sur la biodiversité et sur les services qu'elle rend. Souvent associé par le grand public à des problèmes d'ordre climatique, le terme changement global inclue également la surexploitation des ressources naturelles et les changements d'occupation des sols (Houghton 1996 : IPCC1996).

Malgré la difficulté de distinguer les changements climatiques d'origine naturelle de ceux dus à l'homme, il est aujourd'hui largement admis que le changement climatique rapide de ces dernières décennies est issu principalement de l'activité anthropique (Figure A.1 et 2; Solomon et al. 2007 ; IPCC 2007, Hurrell and Trenberth 2010). Les températures de surface ont augmenté de 0.75°C depuis le début du 20<sup>ème</sup> siècle, l'augmentation la plus rapide ayant lieu ces dernières décennies (Figure A.1, Hurrell and Trenberth 2010). Ainsi, 12 des 14 années les plus chaudes enregistrées depuis le début du siècle dernier ont eu lieu depuis 1995 (Figure A.1 ; Hurrell and Trenberth 2010).

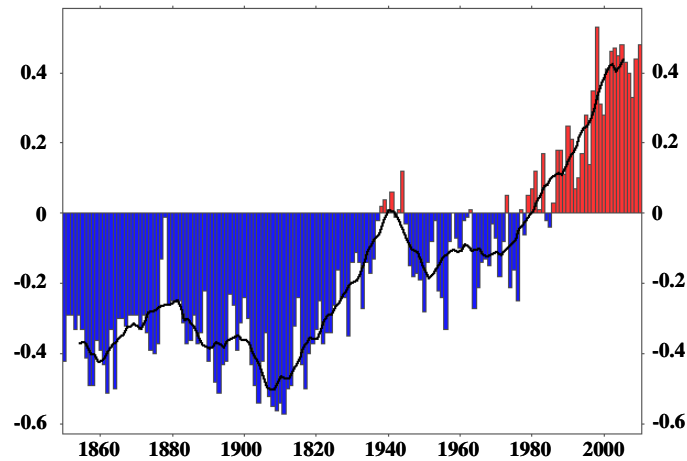


Figure A.1: Anomalies des températures de surface (continents et océans) de 1950 à 2010. Les anomalies sont relatives à la moyenne des températures sur la période 1961-1990. La courbe noire représente les moyennes décennales. Source: Australian Bureau of Meteorology, <http://www.bom.gov.au/>

Cependant, le changement climatique s'effectue de manière hétérogène autour du globe à différentes échelles : latitudinale, longitudinale, altitudinale, etc. (Figure A.2). A titre d'exemples, le milieu terrestre, qui possède une plus faible capacité thermique, se réchauffe plus rapidement que les océans (réchauffement absolu du milieu terrestre : + 0.7°C depuis 1979) et l'hémisphère Nord est davantage touché par l'augmentation des températures que l'hémisphère Sud (Figure A.2 ; Solomon et al. 2007 ; IPCC 2007, Hurrell and Trenberth 2010). De cette hétérogénéité spatiale du réchauffement climatique, découle que les systèmes biologiques seront affectés de manière différentielle suivant leur localisation géographique. Des preuves irréfutables suggèrent que ces changements climatiques récents affectent fortement les systèmes biologiques terrestres (Hughes 2000; McCarthy 2001; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003) mais aussi marins (Hughes 2000; McGowan et al. 2003; Hyrenbach and Veit 2003).



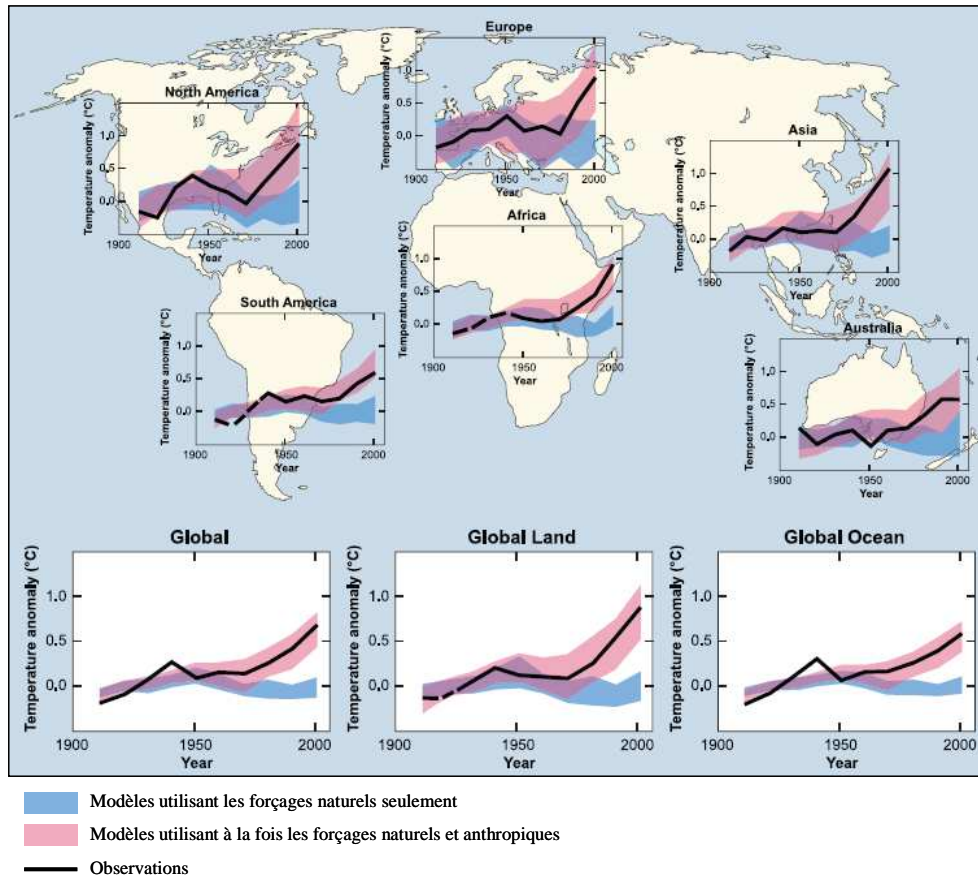


Figure A.2: Comparaison des changements de température observés à l'échelle continentale et globale et des résultats de modèles climatiques utilisant soit uniquement des forçages naturels soit des forçages naturels et anthropiques. Les moyennes décennales relatives à la moyenne sur la période 1961-1990 sont indiquées sur la période allant de 1906-2005 (courbe noire). Les bandes bleues montrent l'intervalle de confiance 5-95% de 19 simulations de cinq modèles climatiques utilisant les forçages naturels dus à l'activité solaire et aux volcans. Les bandes roses montrent l'intervalle de confiance 5-95% de 58 simulations de quatorze modèles climatiques utilisant à la fois les forçages naturels et anthropiques. Source: rapport de synthèse, GIEC 2007

Les besoins grandissants en matières premières (bois, eau, énergie, nourriture, etc.) sont à l'origine de la 2<sup>ème</sup> composante du changement global. En effet, ces autres pressions anthropiques sont reconnues comme étant fortement impliquées dans les modifications rapides et profondes des écosystèmes au cours des 50 dernières années (Assessment 2005). L'exploitation des ressources et la pratique de la chasse remontent à l'origine de l'homme mais aujourd'hui cette exploitation des ressources naturelles se traduit par un prélèvement excessif de ressources qui ne permet pas aux écosystèmes de se restaurer. Cette surexploitation peut atteindre de manière locale ou globale la biodiversité. Les modifications d'utilisation des sols à travers l'urbanisation grandissante, la déforestation ou encore l'intensification de l'agriculture induisent également des changements profonds des mosaïques paysagères et de leur fonctionnement biologique. Cependant, l'impact de ces

changements sur les êtres vivants est très variable et dépend grandement de la zone étudiée et des politiques économiques qui y sont menées.

Toutes ces modifications de l'environnement sont susceptibles d'influencer les organismes vivants de manière directe ou indirecte. À terme, les conséquences observées ou prédites de ces changements sont principalement des augmentations ou diminutions d'effectifs voire des pullulations ou des disparitions locales d'espèces ou de populations, des changements phénologiques et des changements d'aires de distribution des espèces (Hughes 2000). Cependant, les trois composantes du changement global interagissent et co-varient. Les changements climatiques et les changements d'usage des sols sont en effet très étroitement liés : les changements climatiques peuvent entraîner des modifications dans la gestion des terres, et il est probable que l'augmentation de l'agriculture intensive et des pollutions associées, l'urbanisation croissante et le développement industriel agissent en retour sur le climat. La surexploitation des ressources naturelles et les changements d'occupation des sols peuvent également se confondre dans les cas de l'accélération de la déforestation et de l'intensification de l'agriculture. Il devient donc difficile aujourd'hui de les dissocier, et d'en prédire les conséquences sur le fonctionnement des écosystèmes et sur la biodiversité.

### **A.1.2. Réponses des organismes au changement global**

Les relations de cause à effet entre le changement global et les récents bouleversements à différents niveaux d'organisation biologique sont difficiles à mettre en évidence du fait de la rareté des données biologiques à très long terme et de la complexité des mécanismes de réponse des populations aux fluctuations de l'environnement (Parmesan and Yohe 2003). Cependant, différents types de réponses ont été rapportés chez de nombreuses espèces animales et végétales (Hughes 2000; Parmesan 2006). Ces réponses peuvent être classées en quatre grandes catégories : les réponses physiologiques, numériques, phénologiques et de répartition (Figure A.3). Les réponses physiologiques et parfois phénologiques ou numériques sont des conséquences directes du changement global, plus particulièrement de sa composante climatique, tandis que les réponses numériques, phénologiques et de répartition sont souvent des effets indirects qui se produisent au travers des changements physiologiques ou au travers de changement des habitats. Dans cette partie, nous aborderons donc succinctement les effets directs des changements globaux avant de nous

attarder davantage sur l'objet de ce manuscrit : les effets indirects à travers les modifications de l'habitat.

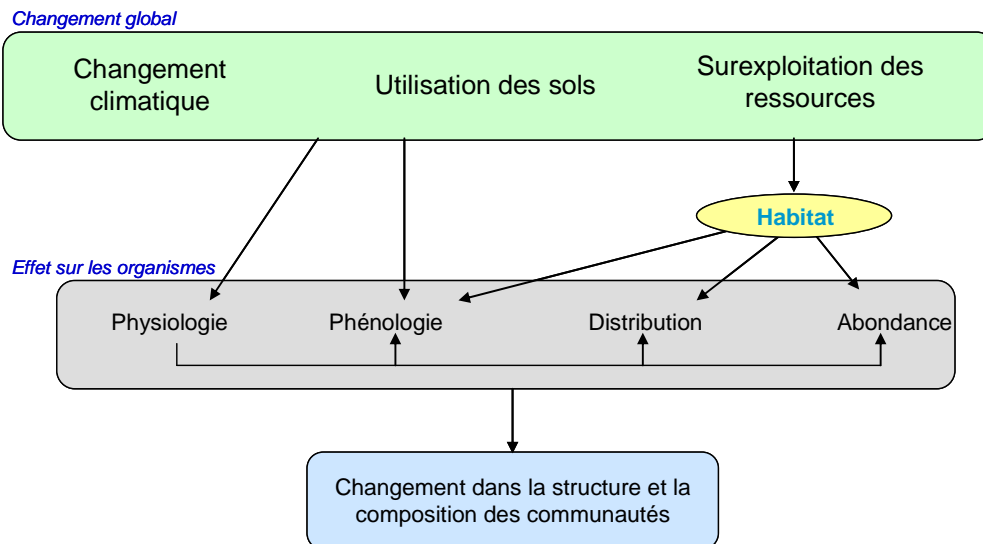


Figure A.3: Principales réponses des organismes face au changement global. Les réponses physiologiques et phénologiques (mais aussi parfois numériques) peuvent être des effets directs du changement global tandis que les réponses numériques, phénologiques et de répartition sont des effets indirects via des changements physiologiques ou au travers de changements dans l'habitat.

### A.I.2.i. Effets directs

Le changement climatique peut agir directement sur les cycles de vie des organismes de par des modifications physiologiques. En effet, de nombreux processus physiologiques tels que la croissance, le bourgeonnement et la floraison des plantes mais aussi les dates de migration et de reproduction (des oiseaux en particulier) sont dépendants des conditions climatiques (Peñuelas and Filella 2001) et sont donc susceptibles d'être perturbés par le changement climatique. Par conséquent, de nombreuses études ont mis en évidence des changements phénologiques en réponse au changement climatique récent (Parmesan and Yohe 2003). A titre d'exemple, en écosystème méditerranéen, les feuilles de la plupart des arbres à feuilles caduques émergent en moyenne 16 jours plus tôt et tombent 13 jours plus tard qu'il y a 50 ans (Peñuelas and Filella 2001). Le règne animal n'est pas épargné. La plupart des espèces britanniques de papillons apparaissent plus tôt dans la saison et ont des périodes de vol plus longues (Roy and Sparks 2000). De nombreuses espèces d'oiseaux entament leur migration pré-nuptiale (Lehikoinen et al. 2004, Lehikoinen and Sparks 2010) et leur reproduction plus tôt dans la saison (Crick and Sparks 1999, Crick 2004, Weidinger and

Král 2007). La plupart des espèces, qu'elles soient animales ou végétales, répondent donc directement au changement climatique par des avancées ou retards dans la phénologie de leurs activités. En plus des changements phénologiques, d'autres paramètres physiologiques comme la détermination du sexe des juvéniles (i.e. chez la tortue peinte *Chrysemys picta*, Janzen 1994, chez le Carouge à épaulettes *Agelaius phoeniceus*, Weatherhead 2005), la mise en place des réserves corporelles (Post et al. 1997) et le développement des défenses immunitaires (Bradley et al. 2005) peuvent également être fortement influencés par les conditions climatiques.

La surexploitation des ressources naturelles a, quant à elle, des conséquences directes sur les effectifs de certaines espèces. La surexploitation des ressources halieutiques est, par exemple, la cause de l'effondrement des populations de morue de l'Atlantique *Gadus morhua* au large de la côte Est de Terre-Neuve dans les années 90 (Hutchings and Myers 1994). De manière directe, le changement d'utilisation des sols peut également engendrer, par destruction mécanique ou chimique, une mortalité accrue de certaines espèces ou une réduction de leur succès de reproduction ayant pour conséquence une diminution des effectifs. A titre d'exemple, de nombreuses espèces d'oiseaux nichant au sol en milieu agricole intensif, telle que l'Outarde Canepetière *Tetrax tetrax*, subissent des destructions massives de leurs nichées mais aussi une mortalité accrue des femelles, suite aux travaux mécaniques effectués sur les parcelles de nidification (Bretagnolle et al. 2011).

De nombreuses espèces ont une physiologie peu sensible au changement climatique (i.e. les endothermes ; Kearney and Porter 2009) mais sont davantage affectées de manière indirecte par des modifications de leur habitat dues au changement climatiques mais également aux changements d'utilisation des sols. Depuis de nombreuses décennies, l'étude de la sélection des habitats par les espèces est centrale en écologie comportementale (Cody 1985). Aujourd'hui, la sélection d'habitat et ses variations temporelles et spatiales prend une dimension supplémentaire : sa compréhension permet d'appréhender les conséquences indirectes du changement global sur les organismes. Mes travaux étant largement ancrés dans ce contexte, les parties suivantes s'attacheront à définir l'habitat et à établir un état des lieux des conséquences du changement global à travers les différentes composantes de l'habitat.

## **A.I.2.ii. Effets indirects à travers l'habitat**

L'habitat d'une espèce est un maillon essentiel pour comprendre les réponses des organismes au changement global. Cependant, il s'agit d'une notion complexe faisant intervenir de nombreux facteurs biotiques et abiotiques ainsi que leurs interactions, et cela à différentes échelles spatiales et temporelles. Il s'ensuit qu'étudier l'effet du changement global, lui-même soumis à de fortes variations spatiales et temporelles, sur l'habitat représente un challenge scientifique que nous nous proposons de relever en partie dans ce travail. Au préalable, nous allons définir la notion d'habitat.

### ***A.I.2.ii.a. Définition d'un habitat***

La compréhension des exigences d'une espèce pour un habitat est historiquement l'une des questions centrales dans le domaine de la conservation et de la gestion de la biodiversité et elle l'est encore davantage de nos jours dans le contexte de changement global. Hall et al. (1997) définit un habitat comme l'ensemble des conditions et ressources présentes dans une zone conduisant à la présence, l'occupation (pour la survie ou la reproduction) d'un organisme donné. Malgré l'utilisation fréquente et restreinte du terme habitat au « lieu de vie » (caractéristiques physiques d'un lieu, Hall et al. 1997), cette définition regroupe à la fois les caractéristiques physiques, biologiques et sociales de l'habitat (Figure A.4). L'habitat physique regroupe les caractéristiques abiotiques d'un milieu, telles que la température, l'humidité, la salinité, la photopériode, la topographie et l'altitude mais aussi des caractéristiques biotiques comme la structure de la végétation (densité, hauteur, composition spécifique, pourcentage de sol nu, etc.) qui constitue un milieu particulier pour les animaux terrestres. L'habitat biologique, comme son nom l'indique, concerne les caractéristiques biotiques du milieu et plus particulièrement les relations entre proies et prédateurs ou entre plantes et herbivores. Enfin, l'habitat social regroupe les relations entre individus d'une même espèce ou d'espèces différentes à travers la vie en groupe (pour la recherche alimentaire, la reproduction et le repos, Inman and Krebs 1987), la facilitation (Hurd 1996, Hahn and Silverman 2006) ou encore le mutualisme (Memmott et al. 2007). L'aspect social de l'habitat prend également en compte la compétition intra- et inter-spécifiques (Rosenzweig 1991) ou encore les relations hôte-parasite (Merino and Møller 2010).

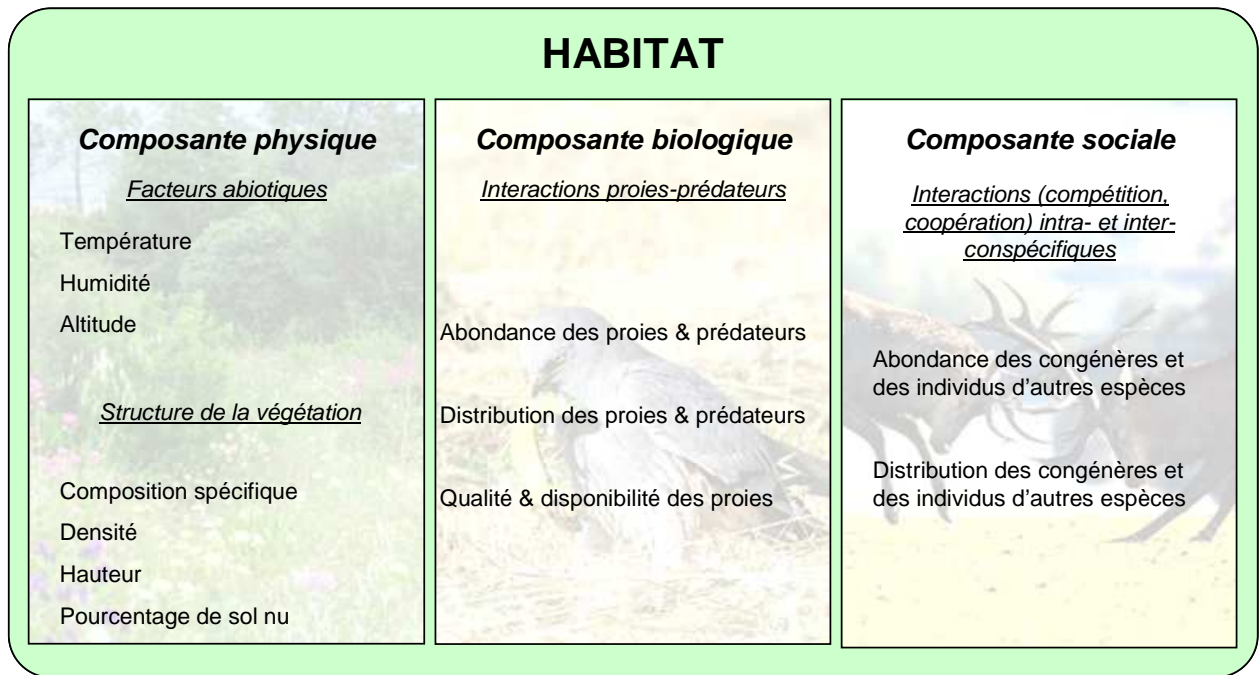


Figure A.4: Description des trois composantes de l'habitat

La distribution des espèces animales n'est donc pas aléatoire (Southwood 1977, Martin 1998, Clark and Shutler 1999, Kolbe and Janzen 2002) et les patrons qui en découlent sont connus pour être le résultat de la sélection naturelle (Southwood 1977, Clark and Shutler 1999). La sélection d'un habitat approprié est donc un processus crucial pour les animaux notamment de par son influence sur la plupart des composantes de la fitness (Danchin et al. 1998, Jones 2001). Afin de sélectionner un habitat, les organismes doivent être en mesure de disperser dans le temps et l'espace (Morris 2011) de manière active ou passive. La sélection d'habitat est un processus spatialement et temporellement hiérarchique par lequel un organisme va choisir quelles composantes de l'habitat il utilisera (Johnson 1980, Hutto 1985, Hall et al. 1997). Ce processus, illustré dans la figure A.5, a été fractionné par Johnson (1980) en quatre échelles spatiales allant de la macro à la micro sélection. Le premier niveau de sélection s'effectue à large échelle spatiale et détermine l'aire de distribution des espèces qui dépend principalement de facteurs abiotiques. Au second niveau spatial (mésos-échelle), les organismes choisissent leur domaine vital (zone dans laquelle les organismes réalisent leurs activités, par exemple un patch de forêt). Le troisième niveau spatial de sélection concerne l'utilisation de composantes particulières (micro-site) du domaine vital (par exemple un arbre pour la nidification). Enfin le quatrième et dernier niveau spatial de sélection concerne l'utilisation d'éléments spécifiques à l'intérieur même des micro-sites choisis au niveau spatial précédent (par exemple une certaine hauteur pour la position d'un nid dans un arbre).

De plus, à méso et micro échelle spatiale, il est important de considérer l'aspect temporel. En effet, les ressources disponibles à ces échelles peuvent varier temporellement et donc influencer sur la sélection d'habitat. Dans le cadre de ce travail de thèse, nous nous sommes intéressés à la sélection de l'habitat à micro et méso-échelle.

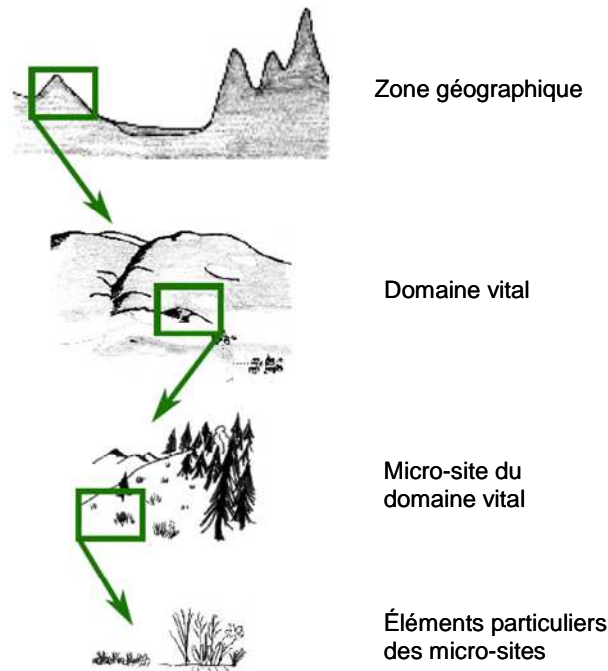


Figure A.5: Illustration du processus spatialement hiérarchique de sélection d'habitat (source: M Basille 2010)

Chaque composante (physique, biologique ou sociale) d'un habitat peut être affectée par le changement global et cela à différentes échelles spatiales. Selon la composante, l'échelle considérée et l'intensité du changement, des modifications de sélection d'habitat peuvent être observables et avoir par conséquent, des répercussions plus ou moins importantes sur la fitness des individus. De nombreuses études ont déjà exploré la réponse des organismes face aux modifications de leur habitat, mais souvent elles se limitent à une ou deux de ses composantes (par exemple : Burger 1987, Stenhouse et al. 2005, Barbaro et al. 2008)). Dans notre étude, nous considérerons les trois composantes simultanément.

### ***A.I.2.ii.b. Réponses des organismes au changement global à travers l'habitat***

Les changements de phénologie, de physiologie, d'abondance et de distributions des espèces, issus des effets directs du changement global altèrent inévitablement l'habitat des organismes et donc de manière indirecte les organismes eux-mêmes. L'altération des habitats se traduit d'une part à travers des modifications des relations entre individus qu'il s'agisse de relations proies-prédateurs (habitat biologique) ou de compétitions intra ou interspécifiques (habitat social) et d'autre part à travers des modifications d'habitat physique : phénologies végétales modifiées, disparition ou apparition d'espèces végétales, modification de la composition floristique, modifications des conditions microclimatiques, fragmentation des milieux. Ces modifications elles-mêmes peuvent être à l'origine d'altérations supplémentaires associées à des changements des pratiques anthropiques comme le calendrier des travaux agricoles (dates de semis, de moissons, etc.).

- *Effets indirects à travers l'habitat physique*

Le changement climatique conjointement au changement d'usage des sols créent des modifications de la structure et des conditions microclimatiques des habitats physiques. Dans les écosystèmes terrestres, ces modifications s'observent notamment au niveau de la structure de la végétation à travers des changements de la composition floristique : les espèces les plus compétitives et adaptées aux nouvelles conditions étant les plus aptes à survivre (McCarty 2001). La densité et la hauteur des couverts mais aussi la croissance et donc la phénologie des plantes peuvent également être affectées à la fois par le changement climatique et le changement d'usage des sols. Ces caractéristiques de la végétation sont utilisées par de nombreuses espèces terrestres comme ressources directes (ressources alimentaires ou pour la reproduction, la protection contre les prédateurs, etc.) ou alors comme indices pour le déclenchement de certaines phases de leur cycle de vie. Leur modification aura potentiellement un impact important pour les espèces utilisatrices. A titre d'exemple, le diamant mandarin *Taeniopygia guttata* utilise l'éruption de pousses de graminées – directement liée à la pluviométrie – comme un indice pour le déclenchement de la reproduction (Zann 1999).



Au-delà des modifications de structure de la végétation, le changement global peut entraîner la perte et la fragmentation des milieux. Les espèces y étant inféodées subissent alors des mortalités directes ou sont forcées à disperser dans de nouveaux environnements pour survivre (Ewers and Didham 2005). L'augmentation de la température ainsi que la diminution des précipitations dans certaines régions entraînent ainsi des changements de distribution de nombreux groupes taxinomiques vers des altitudes plus élevées (McCarthy 2001, Parmesan and Yohe 2003). Cependant, la modification d'un habitat physique peut aussi créer des habitats favorables à de nouvelles espèces. C'est le cas notamment de la déforestation qui peut s'avérer propice à la colonisation d'espèces inféodées à des milieux ouverts.

De la même manière, les changements d'utilisation des terres influencent la structure des habitats physiques et donc les distributions d'espèces et provoquent des migrations et/ou des extinctions (Hobbs 2000). Ces bouleversements de l'habitat physique peuvent également provoquer des diminutions d'abondance des espèces. A titre d'exemple, dans l'Ouest de la France, les populations reproductrices d'Outarde Canepetière *Tetrax tetrax* ont chuté de 96% de 1978 à 2008 dans les milieux agricoles où la surface en prairies constituant leur habitat de reproduction a largement diminué au profit de cultures intensives annuelles créant ainsi une diminution et une fragmentation des milieux favorables à la nidification (Bretagnolle et al. 2011). De plus, dans le cas de cette espèce, l'utilisation du sol a également conduit à une modification de l'habitat biologique par la diminution de la disponibilité des proies, les criquets (Bretagnolle et al. 2011).

- *Effets indirects à travers l'habitat biologique*

Les études concernant les impacts du changement global sur les interactions proies-prédateurs sont relativement rares (Bretagnolle and Gillis 2010, ce chapitre est dans sa version complète à la fin de cette partie). Ce n'est que récemment qu'il est devenu évident d'étudier en profondeur cette relation afin de comprendre et prédire les conséquences du changement global sur les abondances et distributions des espèces (Bretagnolle and Gillis 2010). D'une part, les espèces présentes au sein d'une chaîne trophique peuvent réagir avec des degrés divers au changement de l'environnement (car leurs exigences d'habitat ou les indices régissant leur cycle de vie ne sont pas les mêmes). Il se crée ainsi des décalages phénologiques entre proies et prédateurs (Visser et al. 1998, Pearce-Higgins et al. 2005). A

titre d'exemple, au Pays-Bas, un décalage dû à des printemps plus chauds, entre le pic d'abondance des chenilles de la phalène brumeuse (*Operophtera brumata* L.) et le pic des besoins en nourriture des jeunes Mésanges charbonnières (*Parus major*) a ainsi été observé (Figure A.6; Visser et al. 1998).

Les changements de distribution des espèces peuvent avoir des conséquences complexes car proie et prédateur, ou seulement un des deux peuvent changer leurs aires de distribution. Dans le cas de variations d'abondance dues au changement global, les processus de régulation (bottom-up et top-down) peuvent également être affectés. Par exemple, les populations de Caribou *Rangifer tarandus* ne sont, à l'origine, pas contrôlées par la prédation. Cependant la diminution de leurs ressources alimentaires a entraîné une diminution de la taille des groupes lors des mises bas ce qui a favorisé la prédation des caribous par les loups. Le changement global peut affecter l'abondance des proies donc indirectement le prédateur (Bretagnolle and Gillis 2010) ou le contrôle exercé par le prédateur sur la proie (Stevens et al. 2002, Peach et al. 2004). Il peut ainsi affecter les réponses numériques et fonctionnelles des prédateurs (Bretagnolle and Gillis 2010). Néanmoins, l'impact du changement global sur la relation proie-prédateur et sur les communautés sera dépendant du caractère généraliste ou spécialiste des prédateurs (Bretagnolle and Gillis 2010).

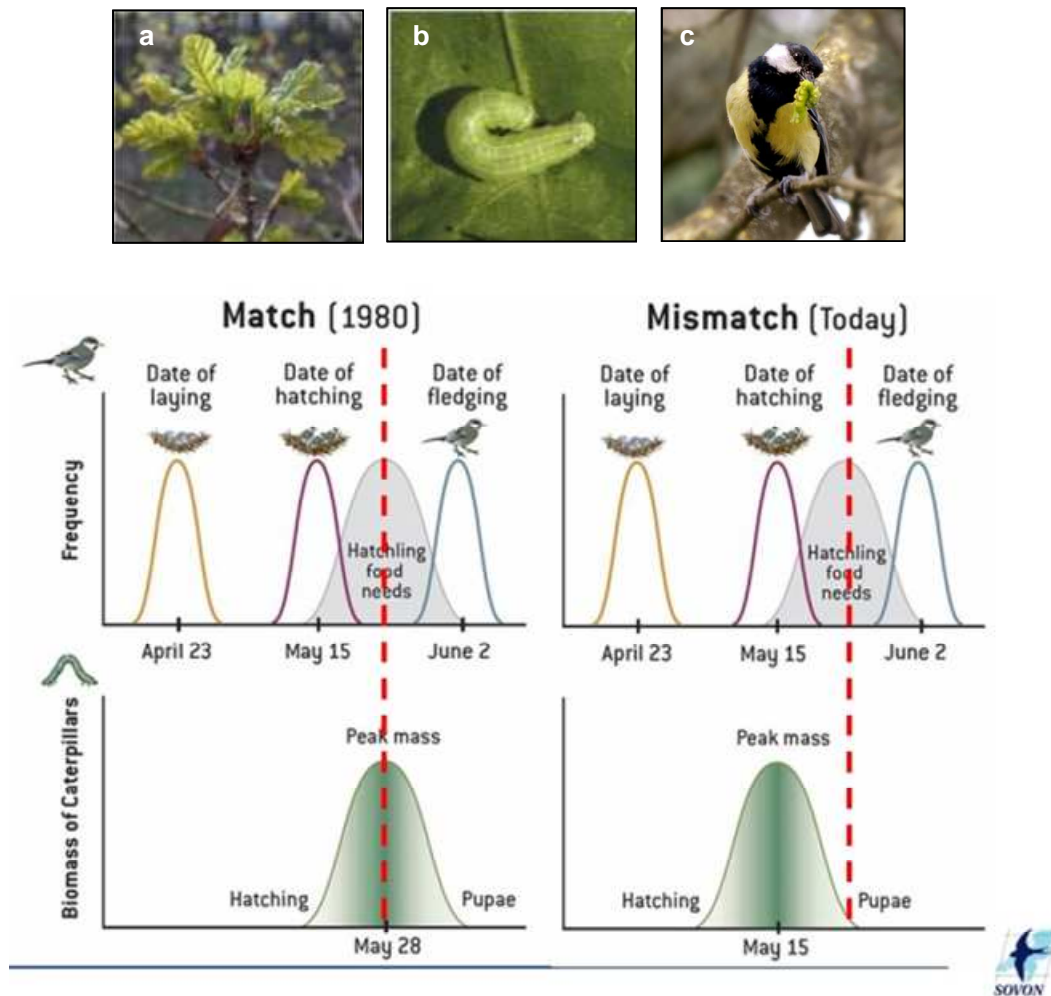


Figure A.6 : phénomène “match-mismatch” observé aux Pays-Bas entre les besoins en nourriture des jeunes mésanges charbonnières *Parus major* et le pic d’abondance de leur proie: les chenilles de phalène brumeuse *Operophtera brumata*. L’augmentation des températures printanières et l’avancée consécutive de l’émergence des feuilles de chêne pédonculé *Quercus robur* (a) a provoqué une avancée de l’apparition des chenilles (b). En revanche, la phénologie de reproduction de la mésange charbonnière n’a pas avancée, au point de créer un décalage entre l’abondance de nourriture et besoins des jeunes. (Photo a : C. Both, b : M.E. Visser, c : E. Pollet), adapté de Visser 2005

### **Changement climatique et interactions proie-prédateur**

Cette thématique a fait l’objet du chapitre de livre suivant intitulé « Effects of Climate Change on Birds », édité par Anders Pape Møller, Wolfgang Fiedler et Peter Berthold et publié en 2010 par « oxford University Press ».

## CHAPTER 16

# Predator—prey interactions and climate change

Vincent Bretagnolle and Hanneke Gillis

## 16.1 Introduction: climate change and trophic networks

Climate change will probably affect the populations of many species (Parmesan and Yohe, 2003; Root *et al.*, 2003; Møller *et al.*, 2004; this volume). Although the magnitude and timing of temperature increases are debated, most predictions qualitatively agree that global warming will cause species extinctions and increase disease transmission (Harvell *et al.*, 2002; Chapters 15, 18). Birds have been found to advance their breeding phenology (Visser *et al.*, 2004; Chapter 11), while bird distribution ranges have not changed dramatically yet (Böhning-Gaese and Lemoine, 2004; Chapter 18). Climate change is likely to impact all trophic levels (Chambers *et al.*, 2005), although the response of communities and ecosystems to climate change has only recently received its deserved attention (but see Harrington *et al.*, 1999). Multi-species interaction networks (i.e., predation, parasitism, and pollination) cannot be assumed to be linear interactions between two or more species, and indeed species may interact with many others, while these interactions may differ in sign, being either positive (i.e. facilitation) or negative (inhibition). Interactions include those between species (Harrington *et al.*, 1999), between traits (e.g. Genner *et al.* (2010) for a long-term study on fish), and between biotic (e.g. density dependence and habitat choice) and abiotic (e.g. temperature) components of global change (Martin, 2001). Interaction strength is also functionally important with regard to ecosystem processes because it encompasses transfer of energy through an ecosystem, a particu-

larly important feature for community stability (Paine, 1980). Climate change is further expected to affect the magnitude of species interactions themselves (review in Tylianakis *et al.*, 2008). Biotic interactions are known to play a major role in the maintenance of ecosystems (Bascompte *et al.*, 2006). It is currently expected that climate change will affect species more through shifts in ecosystem functioning (e.g. pollination, mutualism, and parasitism) than by its direct effect (Rand and Tschardtke, 2007; Tylianakis *et al.*, 2008). Furthermore, compensatory mechanisms that are common in complex networks of biotic interactions (Brown *et al.*, 2001) are generally involved in ecosystem resilience. The latter may become critical under expected global change (Suttle *et al.*, 2007), as complex interactions may buffer the effects of climate change on species.

However, the vast majority of studies analysing bird responses to global warming have so far concerned single species. More recently, it has become obvious that analysing a single variable (often temperature) for a single life stage of a few selected species may not be satisfactory for understanding and predicting the consequences of climate change on the abundance and distribution of birds. A first caveat was revealed by the simple fact that documented advances in breeding phenology of predators may not be in phase with those of their prey (Visser *et al.*, 2004). Examples of differences in phase among trophic levels come from birds feeding on insects that have typically advanced their breeding phenology less than their prey (Visser *et al.*, 1998; Pearce-Higgins *et al.*, 2005), from zooplankton and phytoplankton abundances that have changed at different rates

(Winder and Schindler, 2004), and from animals and plants that have responded heterogeneously to climate change, resulting in increasing asynchrony (Visser *et al.*, 1998; Nielsen and Møller, 2006; Both *et al.*, 2009). A second caveat consists of viewing community response to climate change as the sum of the responses of each individual species (Böhning-Gaese and Lemoine, 2004; but see Post and Forchhammer, 2002), thus considering communities as a 'super organism' with its own climate envelopes (Hole *et al.*, 2009). This view has been challenged because it is too simplistic and to a large extent unrealistic, especially for forecasting community change due to global warming (Wilmers *et al.*, 2007; Chapter 18). Indeed, (1) variation in geographic ranges in response to climate change are known to vary in magnitude between taxa belonging to different trophic levels, or to different taxonomic ranks (Huntley *et al.*, 2004); (2) species ranges were shown to result not only from the direct physiological effects of climate (Porter *et al.*, 2000) but also from indirect effects (Pincebourde *et al.*, 2008); (3) being a consequence of (1), it is reasonable to assume that climate change will affect the temporal and spatial association between interacting species at different trophic levels (Böhning-Gaese and Lemoine, 2004) because species often show their own response to temperature (climatic niche envelopes); and (4) range shifts may have cascading effects on community structure and the functioning of ecosystems (Lovejoy and Hannah, 2005). It is thus extremely likely that the impacts of species range shifts will go far beyond that arising from just adding species to or subtracting species from ecosystems. Such changes may produce trophic cascades or lead to ecological catastrophes such as ecosystem phase shifts, as exemplified by the phase shift of coral reefs from coral to macro-algal dominance (Bruno *et al.*, 2009). How such changes will resonate at the ecosystem level are particularly difficult to predict and surely represents a challenge for ecologists. Therefore, it is becoming clear that the response at the community level can be expected to differ from species-level responses, and the response of one species can hardly be used to predict the response of another, particularly if the latter belongs to another trophic level.

If we are to understand and predict community or species assemblage responses to environmental variability, we must explicitly use a mechanistic

approach including species interactions (Voigt *et al.*, 2007). Any oversimplification, such as reducing climate change to single species stories, may thus lead to inaccurate predictions at best (e.g. estimates of species loss due to climate change vary between 3 and 78%: Thomas *et al.*, 2004), or to wrong predictions at worst (e.g., Böhning-Gaese and Lemoine, 2004), especially so at higher trophic levels. Understanding how climate change will influence the structure of communities and ecosystems, and ecosystem functioning and services has thus become a major pre-occupation for both scientists and managers (Mace *et al.*, 1999). However, climate change effects on species interactions have only started to be studied (Poulsen *et al.*, 1998). The limited theoretical implications of climate change on interacting species that have been investigated so far suggest that density dependence and species interactions may play major roles in determining the magnitude of changes in population density in response to climate change. At the population level, climate change may have important consequences for population regulation, and incidentally the old question of the respective roles of biotic vs. abiotic factors in shaping the regulation of populations and the structure of ecosystems has been revived (Martin, 2001). The observed effects of climate change on distributions of species has led to the suggestion that biotic factors may be less important than abiotic factors (e.g. temperature), although perhaps more in plants than in animals (Austin, 2002).

In this chapter, we first summarize why and how climate change could affect predator-prey interactions. Second, we review the literature about the impact of climate change on predator-prey relationships in birds. A final section will provide prospects for future studies.

## 16.2 Why and how climate change may affect predator-prey interactions

### 16.2.1 Predator-prey relationships and other species interactions

The effects of climate change on host-parasite interactions have been poorly studied (Møller, 2010; Chapter 15). Temperature effects on parasite and

host physiology (Phoenix and Press, 2005) have variable effects in plant-parasite interaction (Tylianakis *et al.*, 2008). In general, climate change modifies the composition of the parasite community and may cause changes in the nature of the interaction itself (i.e. the virulence of parasites; Chapter 15). A rather similar pattern emerges from the larger number of available studies on plant-herbivore interactions: the mismatch in reproductive phenologies between plants and herbivores is thought to reflect differences in the rate of response to changing climatic conditions according to species and/or trophic level. Nevertheless, climate change effects on plant-herbivore interactions appear to be heterogeneous (review in Tylianakis *et al.*, 2008). Overall, climate change effects on various species interactions are quantitatively important, although variable and heterogeneous, and poorly studied (Tylianakis *et al.*, 2008).

Predator-prey interactions are of paramount importance both at population and at community levels because predation is a major cause of mortality in animals, and it is thus a key process in animal population dynamics (Murdoch *et al.*, 2003) and for the evolution of life-history traits (Doligez and Clobert, 2003). Climate change may affect predator-prey interactions through (1) changes in prey and/or predator abundances, (2) the process of predation itself (including defence against predators), and (3) the community level through trophic cascades and regime shifts. Much like plant-herbivore relationships, predator-prey interactions can be altered by phenological changes (Visser *et al.*, 2004). It is also common that these two latter interactions actually interact themselves, and often the responses to rising temperature for plants, herbivores, and predators have effects on phenology (either positive or negative), resulting in strong effects on both herbivore and predator population sizes (Durant *et al.*, 2007). However, predators at higher trophic levels are usually disproportionately affected by environmental perturbation compared to plant-herbivore interactions, be it climate change, competition from invasive species, or habitat modification in general (Voigt *et al.*, 2007). Climate change could affect all species interactions in a community; however, given the key functional role of predators, the effects of climate change on community structure and func-

tioning may be driven by the effects of climate change on predators.

### 16.2.2 Processes and mechanisms by which global warming may affect predator-prey interactions

Climate parameters have been shown to affect predator-prey relationships: Examples include the Moran effect (synchronizing pattern of population fluctuations in space: Ranta *et al.*, 1999), or large-scale climatic fluctuations such as the El Niño Southern Oscillation (ENSO) or the North Atlantic Oscillation (NAO) (Stenseth *et al.*, 2002). For example, the interaction between snowshoe hare *Lepus americanus* and lynx *Lynx canadensis* varies geographically with regions spatially defined by the influence of NAO (Stenseth *et al.*, 1999). Therefore, it is not surprising that if and when climate changes, predator-prey interactions are also affected. Climate may affect species directly through a change in life-history parameters (such as adult survival or fecundity), a shift in geographic range or phenology, or indirectly through the food (prey) of the predator (affecting its abundance: Both *et al.*, 2006), or through the control exerted by the predator on prey (Stevens *et al.*, 2002; Peach *et al.*, 2004). Disentangling the relative contributions of trophic (indirect) and direct climate effects is critical if we are to understand and, more importantly, predict climate driven effects at the community (or species interaction) level.

Typically, predator-prey dynamics are described by quantifying changes in the abundance of prey populations as a consequence of direct consumption by predators (the functional response), and the resulting changes in predator abundance as a consequence of energy transfer from prey to predator breeding (the numerical response; Abrams and Ginzburg, 2000). The modulating effect of climate on this dynamic has recently received considerable attention. In particular, climate affects consumption rates (Stenseth *et al.*, 2005), and thus the dynamics of predator-prey interactions (Post and Stenseth, 1999; Stenseth *et al.*, 1999). Climatic effects may be as important as top-down or bottom-up effects in shaping predator-prey dynamics (Vucetich and Peterson, 2004). In addition, more subtle changes

may be expected, as predators also have non-lethal effects on their prey (Peckarsky *et al.*, 2008) that may also be affected by climate change.

In this section, we provide an overview of the mechanisms by which climate change may affect predator–prey relationships, through the interacting species themselves (i.e. the ‘interactors’) or through different aspects of the relationship (i.e. the ‘interaction’), such as numerical and functional responses, or finally through its effects at the community level (e.g. trophic cascade). There are some processes that are particular to predator–prey relationships, and other processes that are general to any population. Here we list these processes but particularly emphasize those that may be restricted to either predators or prey. Expected changes on prey or predators may include the following:

1) **Changes in distribution.** Changes in distribution may have complex consequences because both prey and predator, or only one of these, may show a shift in distribution range. The spatial shift may, or may not, be associated with a temporal shift (latitudinal or altitudinal gradient). Temporal shifts are dealt with below.

2) **Changes in phenology.** Depending on whether, and to what extent, temperature is a direct cue of processes affecting the population dynamics of the prey and/or the predator, climate change may result in either a temporal mismatch or a closer match between predation and prey. Possibly as a consequence of differential changes in species geographic distribution, or through a change in environmental conditions, several processes could alter the timing of predation events (e.g. prey and predator encounters), which could have strong direct ecological implications or indirect behavioural consequences (through non-lethal effects). Because temporal and spatial shifts, although caused by different climate proxies, will result in patterns of predator–prey interaction that are similar, they will be dealt with simultaneously. The major expected outcome of these spatio-temporal shifts would be stronger or weaker trophic interactions resulting in lower/higher prey and predator abundances.

3) **Changes in population density.** Population sizes and densities of both predator and/or prey may change as a consequence of the direct effects of

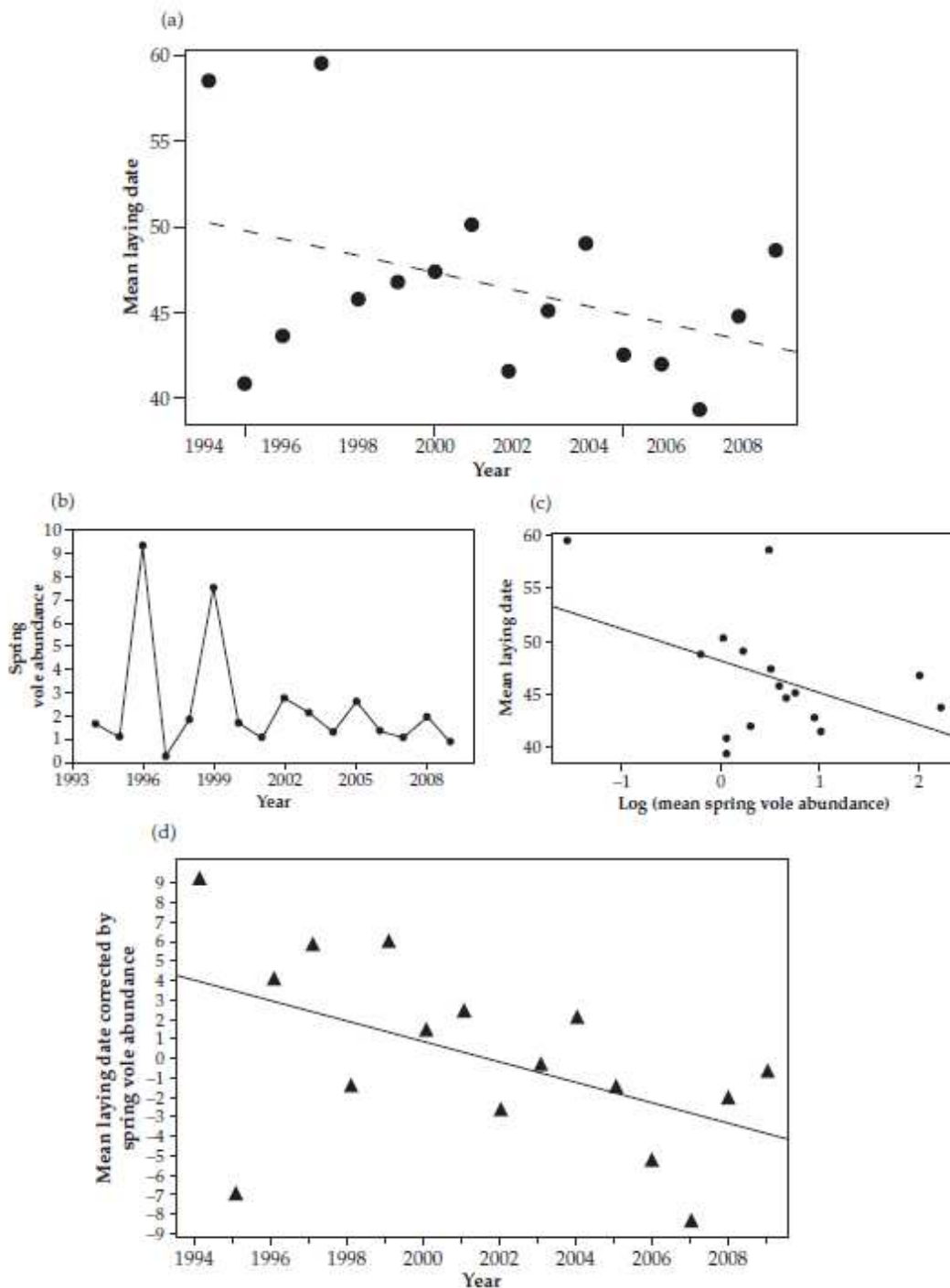
environmental gradual change (temperature rising) or extreme environments (catastrophic events). These changes will occur through climate impacts on vital rates (i.e. survival, breeding success, and dispersal rates). In response, population sizes may change as predicted by classical deterministic models (Murdoch *et al.*, 2003). The direction and magnitude of these changes may differ depending on the shapes of functional and numerical responses (Abrams and Ginzburg, 2000), thus varying with the degree of specialization by the predator and the efficiency of energetic transfer. Therefore, this will affect the ratio between numbers of predators and prey. Yet, this ratio is of considerable interest here, as a ratio-dependent functional response has been suggested to be more sensitive to the interaction than the Holling functional response (Abrams and Ginzburg, 2000).

4) **Changes in behaviour, morphology, or physiology.** These are more subtle changes that are nevertheless expected to be induced by climate change, either through phenotypic plasticity or through micro-evolution. For instance, diurnal activity patterns of predation behaviour may be affected by climate change, with predators or prey having to cool themselves in particular habitats, or through energetic consequences for individuals. As environmental conditions change, populations may respond by progressively changing their morphological characters (e.g. body size), due to either energetic constraints or physiology.

Below we detail these mechanisms.

### 16.2.3 Spatio-temporal effects of climate change on predator–prey interactions

Climatic warming has the potential to affect the spatial and temporal coincidence of organisms, both potentially leading to disrupted synchrony between predators and prey. Overall, there has been a rapidly growing body of literature exploring how disrupted synchrony affect plant–herbivore interactions (e.g. Bale *et al.*, 2002) and predator–prey interactions (e.g. Logan *et al.*, 2006). While changes in prey reproduction could potentially change predator reproduction, recent studies have indicated that predators mainly those preying on insects become



**Figure 16.1** Trends in breeding phenology of a predator (Montagu's harrier *Circus pygargus*) and its prey (common vole *Microtus arvalis*) in western France (Bretagnolle *et al.*, unpublished data; see Millon *et al.* (2008) for details on study site and methods). (a) Pattern of variation in mean laying date (in Julian days: 1 = 1 April); the trend is not significant ( $F = 2.64$ ,  $P = 0.13$ ). (b) Spring common vole abundance (no. ind/100 traps) from 1994 to 2009. (c) Relationship between mean laying date and log-transformed spring vole abundance ( $F = 3.62$ ,  $P = 0.07$ ). (d) Pattern of variation in mean laying date corrected by spring vole abundance; the trend is significant ( $F = 5.04$ ,  $P = 0.04$ ).



increasingly mistimed in terms of their reproduction relative to the timing of reproduction of their prey (Nielsen and Møller, 2006; Both *et al.*, 2009; Chapter 11).

It is also known, although the evidence remains scarce, that climate change affects, more or less rapidly, plants, insects, and birds because of their differential reaction to photoperiod and temperature (reviews in Both *et al.*, 2009; Chapter 11). Both *et al.* (2009) found in a three-trophic-level study (caterpillar, four species of passerines that prey on caterpillars, and a raptor that preys on the four passerines) that caterpillar phenological response to temperature rising through budburst was on average a delay of only 0.25 days, while passerines lagged 0.5 days after the peak in caterpillar abundance. The sparrowhawk *Accipiter nisus* had the largest mismatch of all species considered, which doubled over the 20-year study period. For all three interactions between phenological responses of predators and their prey, evidence was found for a decrease in synchrony over time, probably due to climate change.

Despite many studies having investigated how climate change has and will affect species distribution ranges, none has specifically investigated how differential shifts in range may affect predator-prey interactions. It remains unknown whether distribution shifts are more pronounced in predators than in prey, although this is unlikely since many birds (such as passerines in temperate communities) are both predators (of insects) and prey (of raptor eating birds). However, it has often been suggested that body size may affect the shift in range because larger-bodied species may be more resistant to adverse climate and thus less prone to move (Brommer, 2008), although some studies maintained that larger species may have a poorer ability to respond to environmental changes than smaller species (Stevenson and Bryant, 2000). Raptors eating birds, reptiles, and small mammals are, on average, much larger than their prey, so one may expect that raptors are less susceptible than passerines to be affected by climate change. While most studies on birds have focused on small-bodied species (see section 16.3), recent evidence from raptors suggests that large-bodied species are as affected by climate change as smaller ones, with delays in breeding

events or movement shifts towards north similar to those found for passerines (Lehikoinen *et al.*, 2009). In the Montagu's harrier *Circus pygargus*, a raptor specialist of the common vole *Microtus arvalis*, breeding dates were shown to have advanced over the last 15 years when accounting for vole abundance effect on harrier laying date (Figure 16.1).

Although the number of studies available still remains scarce, a general finding is a mismatch between prey and predator phenologies due to climate change.

## 16.2.4 Climate change effects on population dynamics of prey and predator

### 16.2.4.1 Effects on numbers

Predators have long been identified as being limited or regulated by their food supply (e.g. Sinclair and Krebs, 2002). Climate change is likely to impact directly on the abundance of key invertebrate prey for bird predators (Bale *et al.*, 2002). Food availability is a classical limiting factor for the productivity of insectivorous birds (Marshall *et al.*, 2002), and thus its shortage due to global warming may have significant impacts on bird populations, although this has seldom been studied (Pearce-Higgins *et al.*, 2010). Not only mean but also between-years variance in climate variables such as temperature and precipitation are predicted to change. However, the potential impact of changing climatic variability on the fate of populations has remained largely unexamined. In an analysis of 36 plant and animal species spanning a broad range of life histories and environments, Morris *et al.* (2008) examined how sensitive long-term stochastic population growth rates were likely to be affected by changes in means and standard deviations of vital rates in response to changing climate. They found that short-lived species (insects, annual plants, and algae) were predicted to be more strongly negatively affected by increasing variability in vital rate relative to longer-lived species (perennial plants, birds, and ungulates), and there was no additional effect among taxa. However, only two species examined out of 36 could be considered to be predators (a waterbird, the whooping crane *Grus americana* and the tiger salamander *Ambystoma tigrinum*), and, therefore, no conclusion could be established

about whether population dynamics of predators should be more or less impacted by climate change through direct effects on vital rates than prey (Morris *et al.*, 2008).

#### 16.2.4.2 *The complex interplay between density dependence and climate change*

It is becoming increasingly evident that predator population growth is not purely determined by the rate of prey consumption as usually considered in classic models of predator-prey interactions (Lotka-Volterra or logistic models), but that other factors, including social interaction, interference, and territoriality, also come into play. More recently, models incorporating ratio-dependent functional responses have been proposed (Berryman, 1992). A key factor in modelling the dynamics of predators and their prey is density-dependent regulation, which may occur both in the prey and in the predator. For instance, predation rates decrease when predator densities reach their carrying capacity (e.g. Lande *et al.* 2003). For prey, inverse density dependence, or Allee effect, is apparently not rare (Stephens and Sutherland, 1999). Climate change may affect predator numbers, prey numbers, density dependence in predator numbers, density dependence in prey numbers, and density dependence in the prey-predator interaction itself, or, of course, any combination thereof. In addition, non-linearity (Henden *et al.*, 2009) and the interaction between intrinsic density dependence and extrinsic environmental variation remain a major challenge in predator-prey interactions (Turchin, 1995).

The interplay between density-dependent processes (both acting at the prey and the predator levels) and external factors, such as climate, is a classical problem in population ecology, being further complicated by the contrasting effects of different types of predator-prey interactions (i.e. specialist or generalist predators, see below) and atypical dynamics (such as cycles). Also, the directional trend of climate change (both in average and in variance) adds additional complexity in analyses. When these factors and their interactions are not taken into account, they can produce misleading conclusions for the processes at work. A good example is provided by elk *Cervus virginianus* population trends in Yellowstone National

Park, where a decline concomitant to wolf *Canis lupus* reintroduction led to the idea that wolf predation was the key driver of elk decline. However, a more careful analysis (by modelling) concluded that elk decline was influenced by other factors (human hunting harvest and lower than average annual rainfall) rather than wolf predation, which appeared to primarily be compensatory (Vucetich *et al.*, 2005).

Although models and theoretical predictions have been used repeatedly, empirical data (not to mention experimental evidence) are scarce (Wright *et al.*, 2009). While many authors have analysed predator-prey interactions incorporating density dependence (Sutherland, 2006), predation (Jackson and Green, 2000; Evans, 2004), or climate (Asbjørnsen *et al.*, 2005), fewer have analysed them all together (but see Vucetich *et al.*, 2005). Theoretical models of predator-prey interactions have been tested with observational data mainly using organisms with short generation times and rapid dynamics, especially invertebrates from aquatic ecosystems, while terrestrial studies come mainly from cyclic dynamics (e.g. Capuccino and Price, 1995).

Cyclic predator-prey dynamics has been the focus of much research in ecology over the last 50 years. Cyclic population dynamics can be described using simple time-series models, the properties of which can provide some insights into biological processes involved. For instance, an autoregressive model performed on time series (Royama, 1992) allows identifying whether under-compensation, perfect compensation, or over-compensation are involved (see Clutton-Brock *et al.*, 1997 for more details). Climate change is known to be able to drive population dynamics from stable to cyclic dynamics (Coulson *et al.*, 2001) and is also suspected to be the cause of the recent dampening of cycles of small mammals or moths, as well as their predators (review in Ims *et al.*, 2008). Precise quantification of links between climate and cycles (both prey and predator) often rely on limited empirical data. Kausrud *et al.* (2008) found that winter snow, together with density dependence in the net population growth rate, accounted for the observed population dynamics of lemmings *Lemmus lemmus* between 1970 and 1997, and correctly predicted the

observed absence of rodent peak years after 1994. Furthermore, analysing population models of consumer-resource systems suggested that direct density dependence is primarily related to intratrophic interactions, whereas delayed density dependence in time series may be related to biological interactions. Therefore, numerical changes in delayed density dependence (i.e. the second-order autoregressive coefficient) of a predator-prey interaction due to climate change may reflect changes in the strength of the predator-prey interaction (Stenseth *et al.*, 2002).

Using large-scale indices of climatic variability as proxies of climate has allowed much progress in understanding the role of environmental factors on population dynamics (review in Stenseth *et al.*, 2002). The use of such proxies along with long demographic time series has also allowed detailed investigation of environmental variability and its effects on density-dependent regulation. In particular, the variation in the NAO was found to interfere with density dependence and predation (Vucetich and Peterson, 2004; Wilmers *et al.*, 2006) on the population dynamics of mammalian herbivores. In addition, the same factors acted on driving synchrony (Post and Forchhammer, 2004, 2006). Although density dependence, climate, and predation together determine population dynamics, it is clear that mechanistic models are required to understand more thoroughly how these factors interact (Stenseth *et al.*, 2002). Wilmers *et al.* (2007) have developed a modelling framework to explore the effects of different predation strategies on the response of age-structured prey populations under climate change. They showed that predation acts in opposition to temporal correlation in climatic conditions to suppress prey population fluctuations. Ambush predators (e.g. lion *Panthera leo*) were shown to be more effective at suppressing fluctuations in their prey than cursorial predators (e.g. wolf) because the latter are more effective on prime-aged adults (wolves are able to chase prey over long distances, which lions cannot). Therefore, while this may appear counterintuitive, the presence of predator populations may be able to dampen prey population fluctuations, provided that temporal correlation in climatic conditions increases in the future (Wilmers *et al.*, 2007).

## 16.2.5 Climate change and the nature of predator-prey interaction

### 16.2.5.1 Top-down vs. bottom-up control

A general and still debated issue concerns whether predators control prey populations (review in Murdoch *et al.*, 2003). In particular, the question of whether density dependent or density independent (in other words, biotic versus abiotic) factors control prey or predator populations has been revived (Lande *et al.*, 2003). Whether predators control, or even dampen, prey population fluctuations have been mostly evaluated with models, and to a lesser extent with experiments. Limited empirical evidence is based on introductions of carnivores and suggested that predators led to prey declines in about half the cases (Ebenhard, 1988). More generally, prey populations exist at lower densities when exposed to predators (Mech and Peterson, 2002). A meta-analysis of experimental studies suggested that predation usually results in trophic cascades (Schmitz *et al.*, 2000; see section 16.2.5.4). However, the issue of top-down vs. bottom-up control of prey populations is still hotly debated, and evidence so far suggests that prey control the system more often than the reverse (Vucetich *et al.*, 2005).

Regulating processes (either top-down or bottom-up) may change due to climate warming (i.e. predators are not regulating prey currently but could become a regulating factor due to climate change). A nice example is provided by mammalian predator-prey interactions. Although the abundance of migratory caribou *Rangifer tarandus* is not controlled by predation (Vors and Boyce, 2009), wolves can negatively affect prey abundance when caribou are feeding on resources that are insufficient to maintain high densities. This is because under this circumstance behavioural changes of caribou are such that they are unable to swamp predators on the calving grounds. As climate warming induces loss of lichen as a winter-food resource (Cornelissen *et al.*, 2001), migratory caribou may face increased predation pressure in the future. A more complex scenario appears when elk is added to the caribou-wolf interaction because one of the prey is preferred by wolf, but supports higher predation pressure than the other (Vors and Boyce, 2009). A similar scenario is suggested by Millon *et al.* (2009) with regard

to blackbird *Turdus merula* and song thrush *T. philomelos*, both prey of sparrowhawk, possibly leading to reduced thrush populations. In the case of mismatch phenology between prey and predator, it is further conceivable that prey is more prone to respond to temperature increases than the predator because this gives the prey a new way to escape from predation and hence a higher selective pressure on early breeding for prey (Both *et al.*, 2009).

#### 16.2.5.2 Specialist vs. generalist predators

While specialist predators are mainly dependent on a specific prey species, generalist predators are theoretically able to switch among alternative prey according to their current abundance and/or profitability (Andersson and Erlinge, 1977). Generalist predation in particular may either stabilize (Erlinge *et al.*, 1988) or destabilize the community (Holt, 1977; Bonsall and Hassell, 1997), depending on ecological conditions. Generalist predators are theoretically expected to maintain relatively constant vital rates because they can shift to alternative prey (i.e. they respond mainly functionally to variation in the abundance of their preferred prey) and therefore should display more stable populations than specialist predators (Redpath and Thirgood, 1999). Thus, they are expected to cope better with global changes than with specialist predators, which are generally believed to be more sensitive to environmental change than generalists (Rand and Tschardtke, 2007). However, there are very few studies that have shown that specialist predators are more affected by climate change than generalist predators (but see Rand and Tschardtke, 2007).

Most studies on predator-prey interactions involved specialist predators and one or sometimes a few prey species (Korpimäki and Norrdahl, 1991; Nielsen, 1999). In addition, most studies involved cyclic predator-prey dynamics and came from Fennoscandia (Korpimäki *et al.*, 2003; Lehikoinen *et al.*, 2009). The question thus arises whether the findings can be generalized to more complex food webs (Millon *et al.*, 2008). In particular, how generalist predators will respond to changes in their prey community is not predicted by current theoretical models, despite generalist predators probably constituting the majority of

avian predators (review in Valkama *et al.*, 2005). However, a generalist predator may be partly sensitive to changes in diversity or composition of prey communities. In addition, if generalist predators shift from one prey to another in the community, this may affect interactions among species, both at the level of competing prey or at the level of other predators of the trophic network (Millon *et al.*, 2008). Very few empirical studies are, however, currently available, mainly because it is far less easy to deal with a generalist predator that preys on dozens of prey species and have to be monitored over years in order to analyse functional responses (but see Redpath and Thirgood, 1999; Rutz and Bijlsma, 2006; Millon *et al.*, 2008).

#### 16.2.5.3 Functional vs. numerical responses

The functional response of a predator largely determines the effect of a predator on the prey population (Abrams and Ginzburg, 2000). In addition, shapes of both numerical and functional responses of predators have strong effects for prey community stability and composition (Jaksic *et al.*, 1992). Predation plays a major role in shaping the structure and dynamics of ecological communities, and the functional response of a predator is of crucial importance to the dynamics of any predator-prey system by linking the trophic levels. However, quantitative and precise studies of functional response are scarce, in particular in the ornithological literature (review in Valkama *et al.*, 2005). In addition, there is a great deal of debate on the way we measure functional response and how to 'scale up' from local (individual) measurements to a population-level function (Englund and Leonardsson, 2008), and a major difficulty remains to measure functional response in the field at (very) low prey density. Finally, both for mammal and bird predators very few studies have attempted to document variation in the functional response according to season, social status, or sex. Whether climate modulates the functional response is therefore virtually unknown. One exception is an analysis of kill rate of radio-tagged lynx *Lynx lynx* preying on roe deer *Capreolus capreolus* in Norway (Nilsen *et al.*, 2009). The latter found a clear effect of abiotic climatic factors (NAO in this case) on functional response, related to snow cover.

#### 16.2.5.4 Trophic cascades and regime shifts

If climate change impacts upon several trophic levels simultaneously (which is very likely), then wholesale community changes may become evident and constitute a 'regime shift' (Rodionov, 2004). Climate change, while affecting predator-prey interactions, may also affect community structure through a trophic cascade. In terrestrial ecosystems, trophic cascades are expected and result, for instance, from the indirect effect of predators on plants mediated by herbivores (Paine, 1980; Polis *et al.*, 2000). Trophic cascades partly also result from the non-linear (and thus non-trivial) nature of species interactions (McCann, 2007). They provide examples of how indirect effects propagate in communities via consumption of prey by predators. Trophic cascades have, however, been more documented in aquatic ecosystems than in terrestrial ecosystems, the reason being unclear, but perhaps related to simplified interactions within each trophic level in the former. A terrestrial example comes from a long-term study of a three-trophic-level system including grey wolf, moose *Alces alces*, and their winter food resource, balsam fir *Abies balsamea* (Wilmers *et al.*, 2006). The balsam fir increases in abundance with winter snow (in relation to NAO) and influences wolf kill rates of moose, with cascading effects on balsam fir growth (Post and Stenseth, 1999). A virus outbreak in the wolf population allowed testing the transient effects of reduction of predation pressure and climatic variation on the dynamics of this three-level food chain. When wolf numbers dampened, there was a switch from top-down to bottom-up regulation of the moose population, with a stronger influence of climate on moose population growth rate, underlining synergistic interactions between predators (mediated by pathogens) and climate in trophic control. Similarly, a controlled experiment tested how cascading trophic interactions initiated by arthropod predators were affected by changes in rainfall (mimicking climate change) and resulted in leaf litter decomposition changes (Lensing and Wise, 2006).

#### 16.2.6 Adaptation and selection

While most birds apparently have responded to climate change through phenotypic plasticity (e.g. Charmantier *et al.*, 2008), evolutionary responses

have also been documented (Parmesan and Yohe, 2003; Root *et al.*, 2003; Møller *et al.*, 2004; Chapter 12). For example, changes in body size of birds during a period of only 50 years have been detected (Yom-Tov, 2001). Such morphological changes probably reflect the impact of abiotic conditions on natural selection on body size and parallel Bergman's rule of latitudinal trends in body size resulting from consistent latitudinal patterns of natural selection (Yom-Tov, 2001). However, predators are often long lived, or at least longer lived than their prey, and therefore their biological responses to environmental change may be lagged by one or more generations with respect to their prey (Sæther *et al.*, 2005). Predators are also on average larger than their prey, particularly in aquatic ecosystems as well as in birds (but this is not necessarily true for mammalian predators). Stevenson and Bryant (2000) have suggested with a simple energetic model that small-bodied species will be able to advance breeding dates more easily than large-bodied ones as a response to increasing temperature. These two factors may suggest that larger predators (or longer lived, which to a large extent is correlated) may take more time to respond evolutionarily to their changing environment than their prey and therefore may be more vulnerable to climate change in the long term. These differential responses across trophic levels may impact on ecosystem functioning because predators at higher trophic levels may decline more strongly because of the asynchrony with the phenology of their prey (Both *et al.*, 2009). This process may even accelerate, as early-breeding individuals have higher fitness than late-breeding individuals, and therefore selection for early breeding should increase with increasing temperature (Visser *et al.*, 1998, 2004).

Predatory behaviour may also be altered by climate change. For example, the effects of climate change may be on the ability of predators to capture prey. Even more complex scenarios that involve two trophic interactions have been documented. For instance, prey species with a high prevalence of blood parasites have higher risks of predation than species with a low prevalence (Møller and Nielsen, 2007). Predation therefore appears as a factor affecting host-parasite interactions, by depredating hosts that are more likely to be infected, thus reducing parasite transmission.

Finally, it should be borne in mind that predators can also have direct non-consumptive effects (NCEs) on prey populations by causing changes in prey traits such as behaviour, growth, and development (Schmitz *et al.*, 2004). NCE may be equally or more important than consumption for predator-prey population and community dynamics (review in Peckarsky *et al.*, 2008), having indirect effects on other organisms in the community (e.g. Werner and Peacor, 2003) and on ecosystem functions (Schmitz *et al.*, 2008). Notably, NCE also includes changes in local prey abundance as a consequence of predator-induced prey dispersal or aggregation behaviour (Sih and Wooster, 1994). The recognized contribution of NCE of predators for prey population dynamics, although acknowledged (Peckarsky *et al.*, 2008), may also be easily affected by climate change (typically, snow or vegetation cover), but the latter remains to be studied.

Climate change effects on predator-prey interaction can be very complex because it may affect prey, predator, or both, as well as the interaction itself. Clearly more studies are needed in order to suggest any general pattern.

## 16.3 Climate change and predator-prey relationships in birds: the evidence so far

### 16.3.1 Taxonomic bias

Unfortunately, much more work on the effects of climate change on predator-prey interactions is available for mammals than for birds, and in the previous section we have repeatedly referred to predator-large herbivore relationships, involving wolf, Canadian lynx, and, to a lesser extent, European lynx or other smaller predators. In addition, although there is a large literature on small mammal cycles, sometimes involving avian predators (raptors, owls, and skuas), most often mammalian predators are thought to play the key role and have therefore been more studied than their avian counterparts. This is unfortunate because there are fundamental differences between bird and mammalian predators:

1) Raptors are central place foragers, while mammals are not necessarily or only rarely so. Central place foraging leads to differences in the predator-prey

relationship, in particular the spatial aspects of predator-prey encounters (Orians and Pearson, 1979), energetic constraints (Orians and Pearson, 1979), or travel costs.

2) Raptors, like most birds, are socially monogamous, while mammals are mainly polygynous (Caizergues and Lambrechts, 1999). As the breeding system may affect population dynamics and, more generally, other life-history traits (Bennett and Owens, 2002), it is likely that climate change would affect predator-prey interactions in different ways for mammalian and avian predators. In addition, despite the growing evidence that climate change will affect species interactions, most studies in birds have dealt with small-sized passerines (Møller, 2002; Peach *et al.*, 2004; Tyliaakis *et al.*, 2008), usually cavity nesters. In particular, many fewer studies have addressed bird predators (Rutz and Bijlsma, 2006; Millon *et al.*, 2008). Although Møller *et al.* (2004) previously identified that there was a lack of studies on predators and predator-prey interactions, not much progress has been made since then. In this section, we choose to separate studies on terrestrial and marine ecosystems because of differences in the availability of data. Indeed, in marine ecosystems data on prey are difficult to collect and are thus scarce, when climate effects are well documented, in contrast to terrestrial ecosystems.

### 16.3.2 Trophic interactions in marine ecosystems

Several studies have focused on the impact of climate change on seabirds, which are often top predators in marine pelagic ecosystems (Wanless *et al.*, 2007). Because of this trophic position, they have repeatedly been used as indicators of the state of marine ecosystems (Wanless *et al.*, 2007). Most seabird studies on the effects of climate change have concentrated on Antarctic seabirds. During recent decades, because of climate change, there have been more El Niño than La Niña events, leading to a generally lower than average Southern Oscillation Index (SOI; Murphy *et al.*, 2007; Chapter 2), and, consequently, the Antarctic peninsula is experiencing some of the most rapid warming in the world (Ducklow *et al.*, 2007; Cresswell *et al.*, 2008). The more positive SOI (Trathan *et al.*, 2007) acts through an increase in sea surface temperature

and sea ice season duration and a decreased sea ice extent (Jenouvrier *et al.*, 2003; Ducklow *et al.*, 2007). This may have important consequences for the entire food web in the southern oceans (Trathan *et al.*, 2007) because these phenomena affect primary production and micro- and macro-biology and cause a decline in the abundance and a change in distribution of krill *Euphausiacea* sp., the major food resource for many Antarctic seabird species (Ainley, 2009). The abundance and accessibility of krill are related to sea ice (Loeb *et al.*, 1997), and thus variation in krill supply may have cascading effects through the food web. If these seabirds are not able to switch to other prey species, population declines would be expected.

#### 16.3.2.1 Spatio-temporal effects of changes in prey abundance and distribution on top marine predators

Barbraud and Weimerskirch (2006) studied a long-term data set (55 years) of dates of first arrival and laying for the entire community of Antarctic seabirds in East Antarctica. Apparently, in contrast to the Northern Hemisphere, arrival and laying dates of Antarctic birds are delayed as a consequence of the reduced krill abundance and the delayed access to colonies because of late sea ice break-up (Barbraud *et al.*, 2008). King penguins *Aptenodytes patagonicus* forage over the polar front and dive to the thermocline to feed on myctophid fish (Charrassin and Bost, 2001). Climate change affects the position of both the polar front and the thermocline. This example shows that climate change in marine ecosystems through modifications of sea temperature and sea ice extent in polar regions impacts not only horizontal but also vertical prey distribution. In both studies, the distance to the foraging places is affected and, if increased, may have a negative impact on breeding success (Durant *et al.*, 2007) because of longer foraging trips during the breeding season and thus reduced parent and chick body conditions (Trathan *et al.*, 2007). In the Northern Hemisphere, Atlantic puffins *Fratercula arctica* have been affected by climate change along the Norwegian coast (Durant *et al.*, 2007). This species mainly feeds on herring *Clupea harengus* for which the distribution of larvae is determined by currents. Climate change has already increased water temperature in the Norwegian Sea and thus modified currents and shifted the herring stock to the north far away from

breeding grounds of puffin, thus creating spatial mismatch between prey and predator (Durant *et al.*, 2007). This spatial mismatch might again lead to longer foraging trips and, as a consequence, lower breeding success (Trathan *et al.*, 2007).

#### 16.3.2.2 Effect of climate change on top marine predator life-history traits and predator density

In the Southern Ocean, some marine predator populations show periodicity in population and breeding performance, driven by physical forcing from, for example, the ENSO (Jenouvrier *et al.*, 2005, 2009; Ducklow *et al.*, 2007). During the late 1970s, change of population periodicity and sudden population decrease/increase have been recorded, indicating a regime shift in the Southern Ocean (Jenouvrier *et al.*, 2005; Chapter 2). Such changes to ecosystem structure and functioning observed during ENSO events or regime shifts suggest the potential for long-term changes due to climate change. In several penguin and petrel species (i.e. Adélie penguin *Pygoscelis adeliae*, emperor penguin, and southern fulmar *Fulmarus glacialisoides*), changes in winter conditions (warmer sea surface temperature and lower sea ice concentration) led to a decrease in krill abundance in their foraging areas, causing declines in adult survival and the proportion of birds attempting to breed (Jenouvrier *et al.*, 2003, 2005). Furthermore, 'during warm anomalies, birds skip breeding probably because the food availability is low and limiting for the highly energy demanding reproductive activities' (Jenouvrier *et al.*, 2003). Cresswell *et al.* (2008) showed that rapid changes in the mean supply and the patchiness of krill, the main prey of macaroni penguins *Eudyptes chrysolophus* in South Georgia, could have an effect on female and chick condition and thus on breeding success. Furthermore, Hahn *et al.* (2007) have predicted that climate change will not affect Antarctic skuas *skuua* sp. directly due to increasing temperature but due to changes in the food web, since their diet consists of meals stolen from other seabirds and chicks of other colonial seabirds. To our knowledge, only one study reported a decline in avian prey quality due to global warming in marine ecosystems. In the UK, Wanless *et al.* (2007) reported that climate change impacted seabirds by affecting the quality of prey. The breeding success of black-legged kittiwakes *Rissa tridactyla* was strongly nega-

tively affected by the low condition of their main prey, the sandlance *Ammodytes marinus*. Here climate change must have acted at lower trophic levels (Wanless *et al.*, 2007).

Hilton *et al.* (2006) studied the effects of climate change on the rockhopper penguin *Eudyptes chrysolome*, a close relative of macaroni penguins, which have experienced a marked population decline throughout most of its circumpolar breeding distribution. They used stable isotope analyses of carbon in time series of rockhopper penguin feather samples dating back to 1861 and examined whether penguin decline has been associated with a shift towards lower primary productivity in the ecosystem. They found evidence for a decreased signature in primary productivity, related to changes in isotope ratios associated with annual variations in sea surface temperature, which has therefore affected the carrying capacity of penguin populations.

Changes in prey abundance, distribution, and quality due to climate change have already been shown to affect seabird life-history traits, and there is generally a spatial mismatch between prey distribution and seabird distribution, leading to increased duration of foraging trips.

### 16.3.3 Bird-predator-prey interactions in terrestrial ecosystems

#### 16.3.3.1 Changes in phenology and its consequences on predators

Most studies of the impact of climate change on terrestrial birds revealed a mismatch between the advanced food abundance peak and the food needs of offspring (Both *et al.*, 2009; Chapter 11). However, some studies reported a match between prey abundance and predator reproduction: For instance, Fayt (2006) studied the breeding success of the insect specialist three-toed woodpecker *Picoides tridactylus* in relation to spring temperature and food abundance. Warmer spring temperature induced an earlier beetle abundance peak, with earlier laying dates and higher productivity of woodpeckers. Nevertheless, these apparent benefits of global warming are thwarted by a weak juvenile dispersal (Fayt, 2006). Eurasian golden plovers *Pluvialis apricaria* breeding in the UK feed mainly on synchronized emergence of craneflies (Tipulidae), a key food resource for both adults and

chicks. The phenologies of both golden plover and craneflies are related to temperature, and these relationships predict that future climate change may reduce golden plover productivity (Pearce-Higgins *et al.*, 2005) because craneflies are cold-adapted invertebrates that make them more vulnerable to increases in summer temperature (Bale *et al.*, 2002). In addition, there is a lag between craneflies and plover response to summer temperature because abundance of adult craneflies is correlated with August temperature the previous year, and thus golden plover population growth rate is negatively correlated with August temperature 2 years earlier. Modelled variation in annual productivity for a future scenario of increasing August temperatures predicted a significant risk of extinction of the golden plover population over the next 100 years (Pearce-Higgins *et al.*, 2010).

When early spring temperatures are high, European insectivorous passerines tend to lay their first egg earlier to match peak food abundance (Cresswell and McCleery, 2003). However, during the incubation period, temperature could decrease and lead to a delayed food peak abundance. Consequently, birds have to synchronize their hatching date to match the food peak abundance. Therefore, great tits *Parus major* modified synchronization strategically by varying clutch size and the onset of incubation after clutch completion (Cresswell and McCleery, 2003).

Climate change has also an effect on the timing of migration (Chapter 9). In North America, southward migration of sandpipers and falcons was expected to be strongly related to timing of snowmelt (Niehaus and Ydenberg, 2006). However, sandpipers seem to respond less strongly than their falcon predators to variation in timing of snowmelt, leading sandpipers (adults and juveniles) to encounter more predators on their stopover sites. These different effects of earlier snowmelt indicate that climate change could alter the ecological dynamics of a predator-prey system (Niehaus and Ydenberg, 2006).

#### 16.3.3.2 Changes in prey accessibility and availability, and effects on predator foraging success

Birds feeding on soil-dwelling invertebrate prey have to forage in dry surface soil as climate change generates high temperature and low rainfall.



Indeed, dry surface soil makes it more difficult for birds to probe, and soil invertebrates tend to bury themselves deeper in the ground and thus become inaccessible to predators (Peach *et al.*, 2004). The induced food shortage has consequences for bird condition and thus for breeding success (see Peach *et al.* (2004) for song thrush and Green (1988) for snipe *Gallinago gallinago*). In these cases, climate change is making prey inaccessible, or at least less accessible, to avian predators. However, some authors reported cases of probable benefits of global warming on the availability of prey to their bird predator in aquatic ecosystems. Stevens *et al.* (2002) described the case of a possible improvement of the snail kite's *Rostrhamus sociabilis* foraging success in an increasing temperature scenario in Florida wetlands. The snail kite is a specialist predator of apple snails *Pomacea paludosa*. Apple snail availability depends on water temperature: at low water temperature, it becomes inactive and tends to bury itself, while at higher temperature apple snails are active and consequently become accessible. Nevertheless, severe drying events render apple snails unavailable for kites (Stevens *et al.*, 2002). If water temperature increases due to global warming, it is easy to imagine a shift in snail kite distribution to the north, advancement in laying, and/or an increase in breeding success due to an improvement in apple snail availability and so in foraging success of snail kites. In crag martins *Ptyonoprogne rupestris*, high temperatures during brood care lower breeding success because drought decreases availability of aquatic insects for offspring (Acquarone *et al.*, 2003). Frederick and Loftus (1993) conducted a study about nest failure in herons in relation to climatic conditions and prey availability in estuarine marshes of the Everglades (Florida). Cold temperatures and high wind speeds were found to be most closely associated with nest failure of great egrets *Ardea alba*. Field observations completed by laboratory experiments showed that these weather conditions strongly spoil marsh fish densities by reducing fish activity and increasing their hiding behaviour. As a result, foraging success of egrets is reduced. In the context of global warming (temperature increase), it is conceivable that foraging success, and accordingly breeding success, may be improved. On the other hand, given the fact that climate

change is not expected to act in the same way everywhere (not necessarily through an increase of temperature), it is difficult to test this hypothesis.

#### 16.3.3.3 Generalist vs. specialist bird predators

Generalist predators are expected to cope with climate change better than specialists (see above). However, the few studies available so far indicate that generalist avian predators are not necessarily able to shift to other prey species (e.g. sparrowhawks in Nielsen and Møller, 2006). Furthermore, in a climate change perspective, some specialist predators, such as snail kites, will have more available prey (Stevens *et al.*, 2002). Two studies involved raptor generalist predators. In Denmark, a long-term study on the European sparrowhawk (Millon *et al.*, 2009), one of the most common predators of the Palearctic, preying on a broad spectrum of small-sized birds was monitored along with its prey showing important changes in composition of the prey community during the last 40 years. Population trends of species constituting the prey community of sparrowhawks for over 20 years were available. Contrary to expectations for a generalist predator, sparrowhawks seemed to be predominantly sensitive to changes in the abundance of their two main prey species only (skylark *Alauda arvensis* and blackbird *Turdus merula*). In demographic terms, changes in composition of the prey community, resulting from climate change, impacted the population dynamics of the predator. In turn, for the prey, high blackbird abundance maintained sparrowhawks at a relatively high density, which pushed song thrushes into a predator pit. In another generalist predator, the common buzzard *Buteo buteo*, Lehtikainen *et al.* (2009) found that climate had a much stronger effect (10 times, using normalized coefficients in generalized linear models) than vole abundance on timing of breeding in the raptor. The buzzard, although breeding at its northernmost range in Finland, should have benefited from climate warming: interestingly that is not the case, as the Finnish breeding population has crashed, possibly partly due to a mismatch between winter global warming on one hand (leading to earlier breeding), but no such warming in summer temperature on the other (leading to poor meteorological conditions during chick rearing and ultimately lower productivity).

Gilg *et al.* (2009) reported a study about the impact of climate change on a cyclic predator-prey population dynamics in the high Arctic. The predators involved are both mammals and birds. The two bird predators are the long-tailed skua *Stercorarius longicaudus* and the snowy owl *Nyctea scandiaca*, which feed almost exclusively on lemmings *Dicrostonyx groenlandicus* and could be classed as specialist predators. Until 2000, lemmings displayed regular 4-year cyclic dynamics, but afterwards the density of lemming has remained at a low level (Gilg *et al.*, 2009). As a consequence, the snowy owl has been absent since 2000. Climate change has been suspected to produce such patterns through a decline towards the north of the duration of the snow-free period and the occurrence of frost-melt events (Cappelen *et al.*, 2001). Gilg *et al.* (2009), by running models with different climate change scenarios, showed that in all cases climate change will lead to an increase in the duration of the lemming population cycle and a decrease in the maximum population densities, which may ultimately lead to local extinction of the predator species.

Overall, therefore, contrary to predictions, studies showed that generalist predators do not cope better with climate change than specialists. In addition, shifts in bird phenology generated by global warming through changes in prey ecology may lead to an imbalance in the prey-predator interaction or adaptation by the predator.

#### 16.3.4 Concluding remarks on the impact of climate change on bird-predator-prey interactions

Studies of the effects of global warming on predator-prey interactions in marine ecosystems have investigated almost exclusively bottom-up processes: Through effect on prey, global warming has been shown to indirectly affect many life-history traits and demographic parameters of seabird predators. However, despite many studies conducted on Antarctic top predators (seabirds and marine mammals), the way the predator-prey interaction has been affected by climate change generally remains unknown. In terrestrial ecosystems, studies mainly focused on match-mismatch processes in insectivorous birds of Europe or North America,

although recently several studies involved raptors. Both in marine and terrestrial ecosystems, climate change has started to affect bird predators: our review suggests that climate warming has already had significant effects on several aspects of avian predator-prey interactions, apparently mainly through strong bottom-up effects (i.e. through prey). However, very few studies have detailed the effects of climate change on both prey and their avian predator, with the exception of tits and caterpillars (Both *et al.*, 2009; see also Nielsen and Møller, 2006), and even fewer have identified by which mechanisms such effects have occurred. Compared to theoretical predictions, as well as to the diversity of studies that have been conducted on predator-prey interactions that involve mammalian predators, studies on birds (either passerines or more rarely raptors) are still in their infancy. Virtually no study on bird predators has attempted to analyse processes that are typical of predator-prey interactions (specialist vs. generalist predator, trophic cascade, and numerical and functional responses). While birds represent the most well-known vertebrates (Boucher and Diamond, 2001), it is somewhat surprising that so few comparative and meta-analyses have been carried out because data sets are already available, even for avian predators.

#### 16.4 Future prospects

Despite the recognized and acknowledged importance of the effects of climate change on trophic interactions, there are too few studies currently available to suggest any clear general trend. In addition, given that the detected effects are sometimes in opposite directions, and that a change in a species may indirectly affect other parts of the community through competition, it is currently almost impossible to predict the future effects of global change at the community level using species interactions, and particularly predator-prey interactions. This is surely a major challenge for the future because most predictive studies have so far considered single species, or, when avian communities were concerned, interactions between species were ignored (inter-specific competition and predation). Below we list areas we believe should be tackled in the near future and/or would shed light on the

predicted impacts of climate change on prey, predators, or the community.

#### 16.4.1 Long-term studies

We need more field studies on the long term: there is a clear need for empirical studies investigating the relationships in complex, natural systems (Abrams and Ginzburg, 2000). Seemingly minor changes to individual interactions can combine to exert important effects on the structure of entire communities. Although there are several models and theoretical approaches that encompass these predicted effects, very few (if any) empirical data support these models, therefore it is important to emphasize the need for maintenance of long-term biological data sets to validate predictions. In addition, new studies should be started and carried out in poorly studied, although important, ecosystems (see Møller *et al.* (2004) for a similar plea): predator–prey relationships in the tropics have not been studied, and actually very few long-term data sets are available from the tropics, where climate change is nevertheless acting (e.g. Chamaillé-Jammes *et al.*, 2008), although possibly less strongly than in polar/temperate regions. Another important issue is the relationship between climate and population cycles: there is growing evidence of a causal relationship between climate change and cycle dampening for small mammals and their predators, but also for insects (Jepsen *et al.*, 2008). Again, long-term studies may reveal unexpected patterns: since the mid-1990s, small mammal cycles have been shown to dampen in Fennoscandia (Ims *et al.*, 2008), but most recent data suggest that cycles may restart again, at least in the boreal zone (Brommer *et al.*, 2009). Finally, we need a better integration between observational, experimental, and modelling studies on mechanisms of species interactions along environmental gradients. There are shared limitations of simplified models, and therefore both experimental studies and empirical long-term time series are needed. Above all, the use of mechanistic approaches, only capable of progressive enhancement, are definitely required (Sutherst *et al.*, 2007).

#### 16.4.2 Modelling and experimental studies

There have been few modelling attempts to predict the effects of climate change on predator–prey rela-

tionships. Such models may help to address complex issues such as trophic cascades, hyper-predation processes, and compensation, so far poorly studied in the context of global warming (but see Emmerson *et al.* (2005) for a model with a simple food chain). While the relative importance of deterministic and stochastic factors has been a central tenet in population ecology for at least five decades (see Coulson *et al.* (2004) for a recent summary), the theoretical debate in predator–prey ecology seems so far to be dominated by deterministic models (but see van der Meer and Smallegange, 2009). In particular, there is a complete lack of modelling work using individual- or behaviour-based models (IBM and BBM) on bird–predator–prey interactions. However, we suggest that simple IBMs with simple trophic relationships, involving one prey and its predator, may help understanding how changes in breeding phenology of prey may have population consequences. Behavioural changes in the predator–prey system, such as functional response, NCEs, or the probability of spatial encounter between prey and predator, should certainly be tackled more efficiently by using IBM or BBM. In addition, modelling studies would help answer questions with regards to the climate warming effects on synchronization of breeding phenologies, and how it will affect population dynamics when individual heterogeneity (and variance in fitness) is taken into account. There is currently a debate on the selective pressures that are involved in the mismatch between prey and their passerine predators (Both *et al.*, 2009), and we suggest that evolutionary models may help disentangling whether prey respond more to climate change than predators in order to escape predators or because the predator shows insufficient response to climate warming.

#### 16.4.3 Evolutionary questions

Given that predator–prey interactions are often viewed as an evolutionary arms race, the effects of global warming on predator–prey interactions beg for evaluating its longer-term, evolutionary implications. For instance, the mismatch in phenology between prey and predator (the most commonly observed effect of climate change on predator–prey interactions in birds) may lead to counterintuitive selective pressures. Although it is largely admitted

that early breeders are individuals of higher quality, late breeders (lower-quality individuals) may, however, be favoured by natural selection under these new regimes. Therefore, this is going beyond the classical question of whether micro-evolution is at work, or if only phenotypic plasticity accounts for the observed variation. For example, it remains to be studied whether predators are phenotypically plastic with regards to prey choice, whether prey is able to cope rapidly with a changing predator community, and at which rate micro-evolutionary change could allow either prey or predator to cope with its changing environment. Thus, we need better analyses of the effects of temporal and spatial climatic variation and quantification of species traits in species interactions. With regards to the interaction itself, apart from being specialist or generalist predators, another gradient of predator strategies has been acknowledged, the income vs. capital breeders dichotomy, which has strong effects on life-history traits of predators. To our knowledge, very few studies have studied whether they may show differential responses to climate change in birds, although this is likely.

#### 16.4.4 Conservation issues

The dynamics of small rodent species, such as voles and lemmings that were previously characterized by large-amplitude regular cycles, has changed more or less simultaneously across Europe recently (Ims *et al.*, 2008). The life histories of diurnal raptors and owls are very much dependent on voles (e.g. Salamolard *et al.*, 2000). Thus, climate change could affect these predators indirectly through modifications in population dynamics of voles (Solonen, 2006). As a consequence, specialist predators of cyclic rodents have already declined (Millon and Bretagnolle, 2008). Changes in small herbivore dynamics have the potential to lead to a regime shift, thus representing a new challenge for the conservation of biodiversity. Moreover, the impact of the rodent cycle is transmitted in the food web by several indirect interactions, such as prey switching by facultative generalist predators to alternative prey. The life histories of predators are seemingly adapted to these interactions (Ims and Fuglei, 2005), but it is unknown to what extent their populations

can be sustained under different dynamics. Models in Gilg *et al.* (2009) showed that prey-predator communities will be severely impacted by climate change.

Predators, because they are at the top of the food chain, occur at lower densities, are often larger-bodied than their prey (at least in birds), and are supposed to be more affected by the adverse effects of climate warming than the rest of the ecosystems. Yet predators are very often emblematic species, for many of them, such as raptors, are already of conservation concern (see e.g. Bennett and Owens (2002) for a comparative analysis on birds). Therefore, there are reasons to pay attention to current change in predator numbers as a consequence of climate change, a new challenge for conservation in the near future.

#### 16.5 Acknowledgements

Thanks to Pablo Inchausti for helpful discussions, and for having improved a first draft, as well as Frédéric Barraquand, Stéphanie Jenouvrier, Alexandre Millon, Anders Møller, Aleksi Lehikoinen, and an anonymous reviewer for their careful reading and comments on successive drafts.

#### 16.6 References

- Abrams, P. and Ginzburg, L. (2000) The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology & Evolution* 15, 337–341.
- Acquarone, C., Cucco, M., and Malacarne, G. (2003) Reproduction of the crag martin (*Ptyonoprogne rupestris*) in relation to weather and colony size. *Ornis Fennica* 80, 79–85.
- Ainley, D. (2009) Sea ice: an introduction to its physics, chemistry, biology and geology. In D.N. Thomas and G.S. Diekmann, eds, *Sea Ice: An Introduction to Its Physics, Chemistry, Biology and Geology*. Blackwell, Oxford, UK.
- Andersson, M. and Erlinge, S. (1977) Influence of predation on rodent populations. *Oikos* 29, 591–597.
- Asbjørnsen, E., Sæther, B.-E., Linnell, J., *et al.* (2005) Predicting the growth of a small introduced muskox population using population prediction intervals. *Journal of Animal Ecology* 74, 612–618.
- Austin, M. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* 157, 101–118.

- Bale, J., Masters, G., Hodkinson, I., *et al.* (2002) Herbivory in global climate change research: Direct effects of rising temperature on insect herbivores. *Global Change Biology* 8, 1–16.
- Barbraud, C. and Weimerskirch, H. (2006) Antarctic birds breed later in response to climate change. *Proceedings of the National Academy of Sciences of the USA* 103, 6248–6251.
- Barbraud, C., Marteau, C., Ridoux, V., *et al.* (2008) Demographic response of a population of white-chinned petrels *Procellaria aequinoctialis* to climate and longline fishery bycatch. *Journal of Applied Ecology* 45, 1460–1467.
- Bascompte, J., Jordano, P., and Olesen, J. (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312, 431–433.
- Bennett, P. and Owens, I. (2002) *Evolutionary Ecology of Birds: Life Histories, Mating Systems and Extinction*. Oxford University Press, Oxford, UK.
- Berryman, A. (1992) The origins and evolution of predator-prey theory. *Ecology* 73, 1530–1535.
- Böhning-Gaese, K. and Lemoine, N. (2004) Importance of climate change for the ranges, communities and conservation of birds. *Advances in Ecological Research* 35, 211–236.
- Bonsall, M. and Hassell, M. (1997) Apparent competition structures ecological assemblages. *Nature* 388, 371–373.
- Both, C., Bouwhuis, S., Lessells, C., and Visser, M. (2006) Climate change and population declines in a long-distance migratory bird. *Nature* 441, 81–83.
- Both, C., van Asch, M., Bijlsma, R., *et al.* (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology* 78, 73–83.
- Boucher, J. and Diamond, A. (2001) *The Effects of Climate Change on Migratory Birds: An Annotated Bibliography*. Atlantic Cooperative Wildlife Ecology Research Network University of New Brunswick, Fredericton, Canada.
- Brommer, J. (2008) Extent of recent polewards range margin shifts in Finnish birds depends on their body mass and feeding ecology. *Ornis Fennica* 85, 109–117.
- Brommer, J., Pietiäinen, H., Ahola, K., *et al.* (2009) The return of the vole cycle in southern Finland refutes the generality of the loss of cycles through ‘climatic forcing’. *Global Change Biology* 15 16, 577–586.
- Brown, J., Whitham, T., Morgan Ernest, S., and Gehring, C. (2001) Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science* 293, 643–650.
- Bruno, J., Sweatman, H., Precht, W., *et al.* (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90, 1478–1484.
- Caizergues, A. and Lambrechts, M. (1999) Male “macho” mammals exploiting females versus male “don juan” birds exploited by females: the opposite-sex exploitation (osex) theory. *Ecology Letters* 2, 204–206.
- Cappelen, J., Jørgensen, B., Laursen, E., *et al.* (2001) *The Observed Climate of Greenland, 1958–99 - with Climatological Standard Normals, 1961–90*. Danish Meteorological Institute, Copenhagen, Denmark.
- Capuccino, N. and Price, P. (1995) *Population Dynamics: New Approaches and Synthesis*. Academic Press, London, UK.
- Chamaille-Jammes, S., Fritz, H., Valeix, M., *et al.* (2008) Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. *Journal of Animal Ecology* 77, 135–144.
- Chambers, L., Hughes, L., and Weston, M. (2005) Climate change and its impact on Australia’s avifauna. *Emu* 105, 1–20.
- Charmantier, A., McCleery, R., Cole, L., *et al.* (2008) Adaptive phenotypic plasticity in adaptative phenotypic plasticity in response to climate change in a wild bird population. *Science* 320, 800–803.
- Charrassin, J. and Bost, C. (2001) Utilisation of the oceanic habitat by king penguins over the annual cycle. *Marine Ecology – Progress Series* 221, 285–298.
- Clutton-Brock, T., Illius, A., Wilson, K., *et al.* (1997) Stability and instability in ungulate populations: an empirical analysis. *American Naturalist* 149, 195–219.
- Cornelissen, J., Callaghan, T., Alatalo, J., *et al.* (2001) Global change and arctic ecosystems: Is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology* 89, 984–994.
- Coulson, T., Catchpole, E., Albon, S.D., *et al.* (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* 292, 1528–1531.
- Coulson, T., Rohani, P., and Pascual, M. (2004) Skeletons, noise and population growth: The end of an old debate? *Trends in Ecology and Evolution* 19, 359–364.
- Cresswell, W. and McCleery, R. (2003) How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *Journal of Animal Ecology* 72, 356–366.
- Cresswell, K.A., Wiedenmann, J., and Mangel, M. (2008) Can macaroni penguins keep up with climate- and fishing-induced changes in krill? *Polar Biology* 31, 641–649.
- Doligez, B. and Clobert, J. (2003) Clutch size reduction as a response to increased nest predation rate in the collared flycatcher. *Ecology* 84, 2582–2588.
- Ducklow, H., Baker, K., Martinson, D., *et al.* (2007) Marine pelagic ecosystems: The west Antarctic peninsula.

- Philosophical Transactions of the Royal Society Series B – Biological Sciences* 362, 67–94.
- Durant, J.M., Hjermann, D., Ottersen, G., and Stenseth, N.C. (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33, 271–283.
- Ebenhard, T. (1988) Introduced birds and mammals and their ecological effects. *Swedish Wildlife Research* 13, 1–107.
- Emmerson, M., Bezemer, M., Hunter, M., and Jones, T. (2005) Global change alters the stability of food webs. *Global Change Biology* 11, 490–501.
- Englund, G. and Leonardsson, K. (2008) Scaling up the functional response for spatially heterogeneous systems. *Ecology Letters* 11, 440–449.
- Erlinge, S., Göransson, G., Högstedt, G., et al. (1988) More thoughts on vertebrate predator regulation of prey. *American Naturalist* 132, 148–154.
- Evans, K. (2004) The potential for interactions between predation and habitat change to cause population declines of farmland birds. *Ibis* 146, 1–13.
- Fayt, P. (2006) Reproductive decisions of boreal three-toed woodpeckers (*Picoides tridactylus*) in a warming world: from local responses to global population dynamics. *Annales Zoologici Fennici* 43, 118–130.
- Frederick, P.C. and Loftus, W.F. (1993) Responses of marsh fishes and breeding wading birds to low temperatures: A possible behavioral link between predator and prey. *Estuaries* 16, 216–222.
- Genner, M., Sims, D., Southward, A., et al. (2010) Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long-scale. *Global Change Biology* 16, 517–527.
- Gilg, O., Sittler, B., and Hanski, I. (2009) Climate change and cyclic predator-prey population dynamics in the high-arctic. *Global Change Biology* 15, 2634–2652.
- Green, R.E. (1988) Effects of environmental factors on the timing and success of breeding of common snipe *Gallinago gallinago* (Aves, Scolopacidae). *Journal of Applied Ecology* 25, 79–93.
- Hahn, S., Reinhardt, K., Ritz, M., et al. (2007) Oceanographic and climatic factors differentially affect reproduction performance of Antarctic skuas. *Marine Ecology-Progress Series* 334, 287–297.
- Harrington, R., Woiwod, I., and Sparks, T. (1999) Climate change and trophic interactions. *Trends in Ecology and Evolution* 14, 146–150.
- Harvell, C., Mitchell, C., Ward, J., et al. (2002) Climate warming and disease risks for terrestrial and marine biota. *Science* 296, 2158–2162.
- Henden, J., Ims, R., and Yoccoz, N. (2009) Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. *Journal of Animal Ecology* 78, 636–645.
- Hilton, G., Thompson, D., Sagar, P., et al. (2006) A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin *Eudyptes chrysocome*. *Global Change Biology* 12, 611–625.
- Hole, D., Willis, S., Pain, D., et al. (2009) Projected impacts of climate change on a continent-wide protected area network. *Ecology Letters* 12, 420–431.
- Holt, R. (1977) Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12, 197–229.
- Huntley, B., Green, R., Collingham, Y., et al. (2004) The performance of models relating species geographical distributions to climate is independent of trophic level. *Ecology Letters* 7, 417–426.
- Ims, R. and Fuglei, E. (2005) Trophic interaction cycles in tundra ecosystems and the impact of climate change. *BioScience* 55, 311–322.
- Ims, R., Henden, J., and Killengreen, S. (2008) Collapsing population cycles. *Trends in Ecology and Evolution* 23, 79–86.
- Jackson, D. and Green, R. (2000) The importance of the introduced hedgehog (*Erimaceus europaeus*) as a predator of the eggs of waders (Charadrii) on machair in South Uist, Scotland. *Biological Conservation* 93, 333–348.
- Jaksic, F., Jimenez, J., Castro, S., and Feinsinger, P. (1992) Numerical and functional response of predators to a long-term decline in mammalian prey at a semiarid neotropical site. *Oecologia* 89, 90–101.
- Jenouvrier, S., Barbraud, C., and Weimerskirch, H. (2003) Effects of climate variability on the temporal population dynamics of southern fulmars. *Journal of Applied Ecology* 72, 576–587.
- Jenouvrier, S., Weimerskirch, H., Barbraud, C., et al. (2005) Evidence of a shift in the cyclicity of Antarctic seabird dynamics linked to climate. *Proceedings of the Royal Society of London Series B – Biological Sciences* 272, 887–895.
- Jenouvrier, S., Thibault, J., Viallefont, A., et al. (2009) Global climate patterns explain range-wide synchronicity in survival of a migratory seabird. *Global Change Biology* 15, 268–279.
- Jepsen, J., Hagen, S., Ims, R., and Yoccoz, N. (2008) Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. *Journal of Animal Ecology* 77, 257–264.
- Kausrud, K., Mysterud, A., Steen, H., et al. (2008) Linking climate change to lemming cycles. *Nature* 456, 93–98.

- Korpimäki, E. and Norrdahl, K. (1991) Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. *Ecology* 72, 814–826.
- Korpimäki, E., Klemola, T., Norrdahl, K., *et al.* (2003) Vole cycles and predation. *Trends in Ecology and Evolution* 18, 494–495.
- Lande, R., Engen, S. and Sæther, B.-E. (2003) Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford.
- Lehikoinen, A., Byholm, P., Ranta, E., *et al.* (2009) Reproduction of the common buzzard at its northern range margin under climatic change. *Oikos* 118, 829–836.
- Lensing, J. and Wise, D. (2006) Predicted climate change alters the indirect effect of predators on an ecosystem process. *Proceedings of the National Academy of Sciences of the USA* 103, 15502–15505.
- Loeb, V., Siegel, V., Holm-Hansen, O., *et al.* (1997) Effects of sea-ice extend and krill or salp dominance on the Antarctic food web. *Nature* 387, 897–900.
- Logan, J., Wolessensky, W., and Joern, A. (2006) Temperature-dependent phenology and predation in arthropod systems. *Ecological Modelling* 196, 471–482.
- Lovejoy, T. and Hannah, L. (2005) *Climate Change and Biodiversity*. Yale University Press, New Haven.
- Mace, G., Balmford, A., and Ginsberg, J., eds. (1999) *Conservation in a Changing World*. Cambridge University Press, Cambridge.
- Marshall, M., Cooper, R., DeCocco, J., *et al.* (2002) Effects of experimentally reduced prey abundance on the breeding ecology of the red-eyed vireo. *Ecological Applications* 12, 261–280.
- Martin, T. (2001) Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? *Ecology* 82, 175–188.
- McCann, K. (2007) Protecting biostructure. *Nature* 446, 29.
- Mech, L. and Peterson, R. (2002) Wolf-prey relationships. In L. Mech and L. Boitani, eds, *Wolves: Behavior, Ecology, Conservation*. University of Chicago Press, Chicago.
- Millon, A. and Bretagnolle, V. (2008) Predator population dynamics under a cyclic prey regime: numerical responses, demographic parameters and growth rates. *Oikos* 117, 1500–1510.
- Millon, A., Arroyo, B., and Bretagnolle, V. (2008) Variable but predictable prey availability affects predator breeding success: natural versus experimental evidence. *Journal of Zoology* 275, 349–358.
- Millon, A., Nielsen, J., Bretagnolle, V., and Møller, A.P. (2009) Predator-prey relationships in a changing environment: the case of the sparrowhawk on its avian prey community in a rural area. *Journal of Animal Ecology* 78, 1086–1095.
- Morris, W., Pfister, C., Tuljapurkar, S., *et al.* (2008) Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* 89, 19–25.
- Murdoch, W., Briggs, C., and Nisbet, R. (2003) *Consumer-Resource Dynamics*. Princeton University Press, Princeton.
- Murphy, E., Trathan, P., Watkins, J., *et al.* (2007) Climatically driven fluctuations in Southern Ocean ecosystems. *Proceedings of the Royal Society of London Series B – Biological Sciences* 274, 3057–3067.
- Møller, A.P. (2002) North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migratory passerine bird. *Journal of Animal Ecology* 71, 201–210.
- Møller, A.P. (2010) Host-parasite interactions and vectors in the barn swallow in relation to climate change. *Global Change Biology* 16, 1158–1170.
- Møller, A.P. and Nielsen, J.T. (2007) Malaria and risk of predation: a comparative study of birds. *Ecology* 88, 871–881.
- Møller, A.P., Fiedler, W., and Berthold, P. (2004) *Birds and Climate Change*. Academic Press, London.
- Niehaus, A. and Ydenberg, R. (2006) Ecological factors associated with the breeding and migratory phenology of high-latitude breeding western sandpipers. *Polar Biology* 30, 11–17.
- Nielsen, O. (1999) Gyrfalcon predation on ptarmigan: numerical and functional responses. *Journal of Animal Ecology* 68, 1034–1050.
- Nielsen, J.T. and Møller, A.P. (2006) Effects of food abundance, density and climate change on reproduction in the sparrowhawk *accipiter nisus*. *Oecologia* 149, 505–518.
- Nilsen, E., Linnell, J., Odden, J., and Andersen, R. (2009) Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. *Journal of Animal Ecology* 78, 741–751.
- Orians, G. and Pearson, N. (1979) On the theory of central place foraging. In D.J. Horn, G.R. Staris, and R.D. Michell, eds, *Analysis of Ecological Systems*, pp. 153–177. Ohio State University Press, Columbus.
- Paine, R. (1980) Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49, 667–685.
- Parmesan, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42.
- Peach, W., Robinson, R., and Murray, K. (2004) Demographic and environmental causes of the decline of rural song thrushes *Turdus philomelos* in lowland Britain. *Ibis* 146, 50–59.

- Pearce-Higgins, J., Yalden, D., and Whittingham, M. (2005) Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae). *Oecologia* 143, 470–476.
- Pearce-Higgins, J., Dennis, P., Whittingham, M., and Yalden, D. (2010) Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Global Change Biology* 16, 12–23.
- Peckarsky, B., Abrams, P., Bolnick, D., *et al.* (2008) Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology* 89, 2416–2425.
- Phoenix, G. and Press, M. (2005) Linking physiological traits to impacts on community structure and function: the role of root hemiparasitic Orobanchaceae (ex-Scrophulariaceae). *Journal of Ecology* 93, 67–78.
- Pincebourde, S., Sanford, E., and Helmuth, B. (2008) Body temperature during low tide alters the feeding performance of a top intertidal predator. *Limnology and Oceanography* 53, 1562–1573.
- Polis, G., Sears, A., Huxel, G., *et al.* (2000) When is a trophic cascade a trophic cascade? *Trends in Ecology and Evolution* 15, 473–475.
- Porter, W., Budaraju, S., Stewart, W., and Ramankutty, N. (2000) Calculating climate effects on birds and mammals: Impacts on biodiversity, conservation, population parameters, and global community structure. *Integrative and Comparative Biology* 40, 597–630.
- Post, E. and Forchhammer, M. (2002) Synchronization of animal population dynamics by large-scale climate. *Nature* 420, 168–171.
- Post, E. and Forchhammer, M. (2004) Spatial synchrony of local populations has increased in association with the recent northern hemisphere climate trend. *Proceedings of the National Academy of Sciences of the USA* 101, 9286–9290.
- Post, E. and Forchhammer, M. (2006) Spatially synchronous population dynamics: an indicator of pleistocene faunal response to large-scale environmental change in the Holocene. *Quaternary International* 151, 99–105.
- Post, E. and Stenseth, N.C. (1999) Climatic variability, plant phenology, and northern ungulates. *Ecology* 80, 1322–1339.
- Poulsen, J.G., Sotherton, N.W., and Aebischer, N.J. (1998) Comparative nesting and feeding ecology of skylarks *Alauda arvensis* on arable farmland in southern England with special reference to set-aside. *Journal of Applied Ecology* 35, 131–147.
- Rand, T. and Tschamtkke, T. (2007) Contrasting effects of natural habitat loss on generalist and specialist aphid natural enemies. *Oikos* 116, 1353–1362.
- Ranta, N., Kaitala, V., and Lindström, J. (1999) Spatially autocorrelated disturbances and patterns in population synchrony. *Proceedings of the Royal Society of London Series B – Biological Sciences* 266, 1851–1856.
- Redpath, S. and Thirgood, S. (1999) Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. *Journal of Animal Ecology* 68, 879–892.
- Rodionov, S. (2004) A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters* 31, L09204.
- Root, T., Price, J., Hall, K., *et al.* (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421, 57–60.
- Royama, T. (1992) *Analytical Population Dynamics*. Springer, New York, NY.
- Rutz, C. and Bijlsma, R. (2006) Food-limitation in a generalist predator. *Proceedings of the Royal Society of London Series B – Biological Sciences* 273, 2069–2076.
- Sæther, B.-E., Engen, S., Møller, A.P., *et al.* (2005) Time to extinction of bird populations. *Ecology* 86, 693–700.
- Salamolard, M., Butet, A., Leroux, A., and Bretagnolle, V. (2000) Responses of an avian predator to variations in prey density at a temperate latitude. *Ecology* 81, 2428–2441.
- Schmitz, O., Hamback, P., Beckerman, A., and Leibold, M. (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist* 155, 141–153.
- Schmitz, O., Krivan, V., and Ovadia, O. (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* 7, 153–163.
- Schmitz, O., Grabowski, J., Peckarsky, B., *et al.* (2008) From individuals to ecosystem function: toward an integration of evolutionary and ecosystem ecology. *Ecology* 89, 2436–2445.
- Sih, A. and Wooster, D. (1994) Prey behavior, prey dispersal, and predator impacts on stream prey. *Ecology* 75, 1200–1207.
- Sinclair, A. and Krebs, C. (2002) Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society Series B – Biological Sciences* 357, 1221–1232.
- Solonen, T. (2006) Overwinter population change of small mammals in southern Finland. *Annales Zoologici Fennici* 43, 295–302.
- Stenseth, N.C., Chan, K., Tong, H., *et al.* (1999) Common dynamic structure of Canada lynx populations within three climatic regions. *Science* 285, 1071–1073.
- Stenseth, N.C., Mysterud, A., Ottersen, G., *et al.* (2002) Ecological effects of climate fluctuations. *Science* 297, 1292–1296.



- Stenseth, N.C., Ottersen, G., Hurrell, J., and Belgrano, A., eds. (2005) *Marine Ecosystems and Climate Variation: The North Atlantic: A Comparative Perspective*. Oxford University Press, Oxford, UK.
- Stephens, P. and Sutherland, W.J. (1999) Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution* 14, 401–405.
- Stevens, A., Welch, Z., Darby, P., and Parcival, H. (2002) Temperature effects on Florida applesnail activity: implications for snail kite foraging success and distribution. *Wildlife Society Bulletin* 30, 75–81.
- Stevenson, I. and Bryant, D. (2000) Avian phenology: climate change and constraints on breeding. *Nature* 406, 366–367.
- Sutherland, W.J. (2006) *Ecological Census Techniques*. Cambridge University Press, Cambridge, UK.
- Sutherst, R., Maywald, G., and Bourne, A. (2007) Including species interactions in risk assessments for global change. *Global Change Biology* 13, 1843–1859.
- Suttle, K., Thomsen, M., and Power, M. (2007) Species interactions reverse grassland responses to changing climate. *Science* 315, 640–642.
- Thomas, C., Williams, S., Cameron, A., et al. (2004) Biodiversity conservation uncertainty in predictions of extinction risk/effects of changes in climate and land use/climate change and extinction risk (reply). *Nature* 430.
- Trathan, P., Forcada, J., and Murphy, E. (2007) Environmental forcing and southern ocean marine predator populations: effects of climate change and variability. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences* 362, 2351–2365.
- Turchin, P. (1995) Population regulation: old arguments and a new synthesis. In N. Cappuccino and P.W. Price, eds, *Population Dynamics: New Approaches and Synthesis*, pp. 19–40. Academic Press, New York, NY.
- Tylianakis, J., Didham, R., Bascompte, J., and Wardle, D. (2008) Global change and species interactions in terrestrial ecosystems. *Ecological Letters* 11, 1351–1363.
- Valkama, J., Korpimäki, E., Arroyo, B., et al. (2005) Birds of prey as limiting factors of gamebird populations in Europe: a review. *Biological Reviews* 80, 171–203.
- Visser, M., Van Noordwijk, A., Tinbergen, J., and Lessells, C. (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London Series B – Biological Sciences* 265, 1867–1870.
- Visser, M., Both, C., and Lambrechts, M. (2004) Global climate change leads to mistimed avian reproduction. *Advances in Ecological Research* 35, 89–110.
- Voigt, W., Perner, J., and Jones, T.H. (2007) Using functional groups to investigate community response to environmental changes: two grassland case studies. *Global Change Biology* 13, 1710–1721.
- Vors, L. and Boyce, M. (2009) Global declines of caribou and reindeer. *Global Change Biology* 15, 1365–2486.
- Vucetich, J. and Peterson, R. (2004) The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. *Proceedings of the Royal Society of London, Series B – Biological Sciences* 271, 183–189.
- Vucetich, J., Smith, D., and Stahler, D. (2005) Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. *Oikos* 111, 259–270.
- Wanless, S., Frederiksen, M., Daunt, F., et al. (2007) Black-legged kittiwakes as indicators of environmental change in the North Sea: evidence from long-term studies. *Progress in Oceanography* 72, 30–38.
- Werner, E. and Peacor, S. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84, 1083–1100.
- Wilmers, C., Post, E., Peterson, R., and Vucetich, J. (2006) Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. *Ecology Letters* 9, 383–389.
- Wilmers, C., Post, E., and Hastings, A. (2007) The anatomy of predator-prey dynamics in a changing climate. *Journal of Animal Ecology* 76, 1037–1044.
- Winder, M. and Schindler, D. (2004) Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* 85, 2100–2106.
- Wright, L., Hoblyn, R., Green, R., et al. (2009) Importance of climatic and environmental change in the demography of a multi-brooded passerine, the woodlark *Lullula arborea*. *Journal of Animal Ecology* 78, 1191–1202.
- Yom-Tov, Y. (2001) Global warming and body mass decline in Israeli passerine birds. *Proceedings of the Royal Society of London Series B – Biological Sciences* 268, 947–952.
- van der Meer, J. and Smallegange, I. (2009) A stochastic version of the Beddington-Deangelis functional response: modelling interference for a finite number of predators. *Journal of Animal Ecology* 78, 134–142.

- *Effets indirects à travers l'habitat social*

Le changement global peut affecter à la fois les interactions sociales intra et interspécifiques. L'assemblage d'espèces en communautés écologiques reflète les interactions entre les organismes mais aussi entre les organismes et l'environnement abiotique (Walther et al. 2002).

Tylianakis et al. (2008) ont listé l'ensemble des interactions interspécifiques pouvant être affectées par le changement climatique. Celui-ci peut provoquer une diminution de la force des interactions mutualistes impliquant les plantes (pollinisation et dispersion des graines ; Memmott et al. 2007). En effet, en perturbant le chevauchement temporel entre la production de fleurs et l'activité de vol des pollinisateurs, il altère l'opportunité des interactions entre les plantes et ces insectes (Wall et al. 2003). Il provoque également des effets multi-trophiques en cascade. Il est en effet largement établi que l'intensification de l'agriculture a des effets néfastes sur de nombreuses composantes de la chaîne trophique des organismes du sol (Hendrix et al. 1986; Wardle 1995), ceux-ci les répercutant sur divers taxa des niveaux trophiques supérieurs. De plus, des changements d'aires de distributions de certaines espèces peuvent venir perturber la composition des communautés en augmentant la compétition entre espèces arrivantes et espèces indigènes ou en altérant la dominance relative d'espèces co-existantes (Davis 2003). Des changements dans l'équilibre compétitif entre espèces végétales peuvent en effet être provoqués par des changements de pressions exercées par des herbivores introduits (Callaway 2006).

D'autre part, les interactions hôte-parasite dépendent de l'abondance respective des hôtes et des parasites, du taux de transmission, de l'effet du parasite sur son hôte et du niveau de défense de l'hôte vis-à-vis du parasite (Merino and Møller 2010). Les changements environnementaux sont susceptibles d'affecter ces trois étapes. Toutefois, les conséquences de ces changements dépendent à la fois du parasite et de l'hôte. En effet, selon l'espèce de parasite, le changement climatique peut réduire ou augmenter l'abondance des parasites et par conséquent affecter les défenses immunitaires des hôtes (Merino and Møller 2010).

Les études concernant l'effet du changement global sur les organismes à travers les interactions intra-spécifiques sont rares voire inexistantes. Cependant, la fragmentation et la dégradation des habitats physiques et biologiques favorables à une espèce peuvent potentiellement provoquer une agrégation des individus et ainsi augmenter la compétition intra-spécifique chez les espèces territoriales ou au contraire favoriser la coopération entre

individus chez les espèces coloniales. A l'inverse, l'isolement de certaines populations ou individus pourraient également être observé suite à une fragmentation des habitats.

Le changement global peut donc affecter les organismes à travers les différentes composantes de l'habitat. Cependant, celles-ci interagissent fortement car l'une influence toujours ou presque l'autre. De ce fait, pour comprendre la sélection de l'habitat et les conséquences de ses modifications (dues au changement global), il est nécessaire de considérer non seulement ses trois composantes mais aussi leurs interactions.

Certains écosystèmes sont davantage affectés par le changement global que d'autres, soit du fait qu'ils sont plus exposés à l'un ou l'autre de ses piliers, soit du fait qu'ils sont exposés simultanément à plusieurs d'entre eux. Les agro-systèmes regroupent à ce titre des milieux particulièrement concernés par le changement global: d'une part, ils sont soumis à la fois au changement climatique et au changement d'usage des sols (à travers les pratiques de l'agriculture intensive) ; d'autre part, ils occupent une surface importante de la planète; et enfin du fait d'un déséquilibre des conflits d'usage en faveur de la production, ils ne font pas (ou peu) l'objet de mesures de protection vis-à-vis des habitats qu'ils hébergent.



## **A.II. DES MILIEUX PARTICULIEREMENT SOUMIS AU CHANGEMENT GLOBAL : LES ESPACES AGRICOLES**

### **A.II.1. Généralités**

Les espaces agricoles représentent 18% de la surface mondiale, plus de 45% de la surface européenne (Food and Agriculture Organisation; <http://faostat.fao.org>, Donald et al. 2006) et 54% du territoire français. Ils sont affectés simultanément par les trois composantes du changement global : changement climatique, surexploitation des ressources naturelles et modification de l'utilisation des sols, les deux dernières étant régies par l'intensification de l'agriculture. Dans l'Union Européenne, l'intensification de l'agriculture (définie comme l'augmentation de la production de matières premières par unité de surface) issue de l'instauration de la PAC (Politique Agricole Commune) a conduit à des bouleversements considérables de ces milieux. Ces bouleversements affectent tous les aspects du paysage agricole. La gestion, le type et l'abondance relative des différentes cultures ont drastiquement changé (Chamberlain et al. 2000). Ainsi, les milieux pérennes ont fait peu à peu place aux cultures intensives annuelles. Les systèmes agricoles sont passés d'un mode extensif de polyculture/élevage à la monoculture intensive aboutissant ainsi à une simplification de la mosaïque paysagère (Figure A.7). Cette dernière est passée d'un système bocager avec des petites parcelles séparées par des haies à des plaines uniformes avec des grandes parcelles et des linéaires de haies réduits. L'intensification se traduit également par l'utilisation massive de la fertilisation et de produits phytosanitaires tels que les herbicides et les insecticides. Les systèmes de rotation des cultures ont également été simplifiés. La phénologie des cultures a aussi été modifiée par les pratiques agricoles mais également par les changements climatiques. A titre d'exemple, le semis des céréales est progressivement passé du printemps à l'automne. Tous ces changements ont été grandement favorisés par le développement de la technologie agricole en termes de machinerie agricole, de sélection et création variétale et de développement de pesticides et d'engrais (Chamberlain et al. 2000).



Figure A.7: Evolution de la mosaïque paysagère de 1958 à 1982 sur la Zone Atelier Plaine & Val de Sèvres (montage A. Thomas & V. Bretagnolle), à partir des photographies aériennes de l'IGN. Noter la simplification du paysage et l'agrandissement progressif des parcelles et la diminution du linéaire de haie.

La conversion des terres de systèmes naturels complexes en écosystèmes agricoles simplifiés est une cause majeure de la perte de biodiversité actuellement observée à l'échelle mondiale (Matson et al. 1997, Tschardt et al. 2005, Flynn et al. 2009). A des échelles nationales ou paysagères, des déclin de la diversité en espèces dus à l'intensification de l'agriculture ont été rapportés chez de nombreux taxa : les mammifères (Sotherton 1998), les insectes (Benton et al. 2002), les plantes (Robinson and Sutherland 2002) et les oiseaux (Donald et al. 2001). A titre d'exemple, 43% des espèces européennes d'oiseaux étant associées aux écosystèmes agricoles ont un statut de conservation défavorable (Tucker 1999). Dans la plupart des pays européens, les oiseaux des plaines agricoles ont décliné davantage que les espèces inféodées à d'autres types d'habitats (Stoate et al. 2003, Figure A.8). En effet, l'intensification de l'agriculture semble coïncider avec le déclin des espèces hivernant ou se reproduisant dans ces milieux (Fuller et al. 1995, Chamberlain et al. 2000). Les causes avancées sont multiples. L'utilisation massive d'herbicides et d'insecticides peut avoir réduit la disponibilité alimentaire pour les oiseaux insectivores et granivores de manière directe ou indirecte (Potts 1986, Campbell et al. 1997, Evans et al. 1997, Brickle et al. 2000,



Chamberlain et al. 2000, Henderson et al. 2000). Les travaux agricoles plus nombreux, effectués plus tôt et avec des machines de plus en plus puissantes peuvent également induire plus de mortalité directe des oiseaux adultes et des destructions de nichées (Chamberlain et al. 2000), Henderson et al. 2000). L'augmentation de l'application d'engrais, la production d'ensilage et le réensemencement généralisé auraient pour conséquence un couvert végétal dense, défavorable à la nidification de certaines espèces d'oiseaux nichant au sol et conduiraient donc à une diminution des habitats de reproduction favorables (O'Connor and Shrubbs 1986, Wilson et al. 1997, Chamberlain et al. 2000, Henderson et al. 2000).

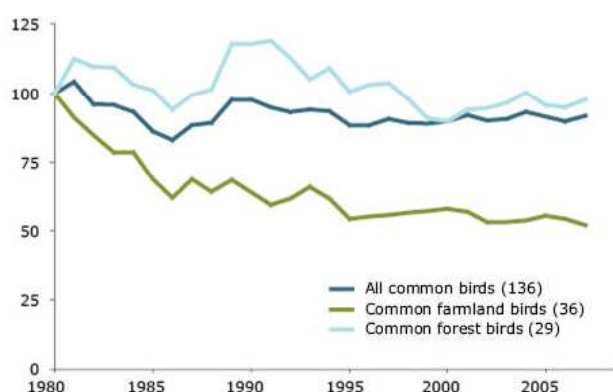


Figure A.8: Evolution de l'indice d'abondance des oiseaux communs d'Europe ces 30 dernières années. 100 correspond à l'abondance en 1980. La diminution la plus drastique est observée chez les oiseaux inféodés aux milieux agricoles. Source: EBCC; RSPB; BirdLife; Statistics Netherlands ; SEBI indicator 01.

Les systèmes d'agriculture intensive offrent aux espèces des habitats particuliers où la structure de la végétation est soumise aux variations des conditions climatiques et d'usage des sols qui peuvent donc à travers des modifications de l'habitat, influencer les composantes de la fitness des animaux qui y sont inféodés. Les espèces dans ces systèmes sont soumises à un environnement fragmenté et changeant d'année en année (changement du type de culture, de la variété et de la phénologie) et au cours d'une même année (croissance des cultures). L'intensification de l'agriculture a conduit à une simplification mais aussi à une homogénéisation de la structure intra-parcellaire de la végétation tout en maintenant des différences inter-parcellaires (différences de type de culture, de densité, de hauteur de végétation dues à des itinéraires techniques et des caractéristiques du sol différents). De manière simplifiée, les organismes vivant dans ce type de milieu ont le choix entre différentes parcelles pour accomplir leurs activités (alimentation, nidifications, etc.).

L'intérêt de ce type de milieu réside dans l'influence simultanée des trois composantes du changement global. Nous avons donc choisi de nous intéresser à ces milieux particuliers. Le site d'étude dans lequel l'ensemble des travaux de cette thèse s'inscrit est donc une plaine agricole intensive, décrite ci-dessous.



## **A.II.2. Zone d'étude : Zone Atelier Plaine et Val de Sèvre**

La Zone « Atelier Plaine & Val de Sèvre » est une plaine céréalière située au sud de Niort dans le département des Deux-Sèvres en région Poitou-Charentes (France, 46°11'N, 0°28'W; Figure A.9). Pour moitié de sa superficie, elle bénéficie aussi du statut de Zone de Protection Spéciale (ZPS, site NATURA 2000 désigné pour la biodiversité remarquable des espèces de la Directive Oiseaux). La superficie de cette zone d'étude s'est progressivement agrandie, passant de 200 km<sup>2</sup> en 1995 à 350 km<sup>2</sup> en 1997 et enfin à près de 460 km<sup>2</sup> en 2007. Elle comprend environ 650 exploitations agricoles, 19.000 parcelles agricoles de taille moyenne (3 ha), dont l'occupation exhaustive des sols est inventoriée depuis 1994 et est disponible dans une base de données spatialisées. Cette plaine est située sur un plateau calcaire drainant qui suite à d'importants remembrements et à l'intensification des pratiques culturales, se compose essentiellement de céréales (blé et orge, 40% de la superficie totale, Figure A.9) mais aussi de maïs, tournesol, pois, colza et quelques prairies (15% des parcelles contre 60% en 1970, Figure A.9). Cependant, deux cordons bocagers dominés par des prairies et des maïs subsistent encore (Figure A.9). Le linéaire de haies est considérablement réduit et fragmenté et se limite essentiellement aux deux cordons bocagers et aux périphéries des villages. Quelques bosquets et bois de superficie modeste persistent encore (3% de la surface totale). L'élevage (bovins, caprins) est encore présent mais en forte diminution. L'intérêt de ce site d'étude réside dans sa taille et son historique de données sur l'occupation des sols et la faune de plaine suivie et étudiée par le CNRS de Chizé (outardes, busards, passereaux, micro-mammifères, insectes, plantes). Ainsi, doté d'une base de données spatialisée, cela en fait un dispositif quasi-expérimental où les parcelles peuvent être considérées comme des répliqués.

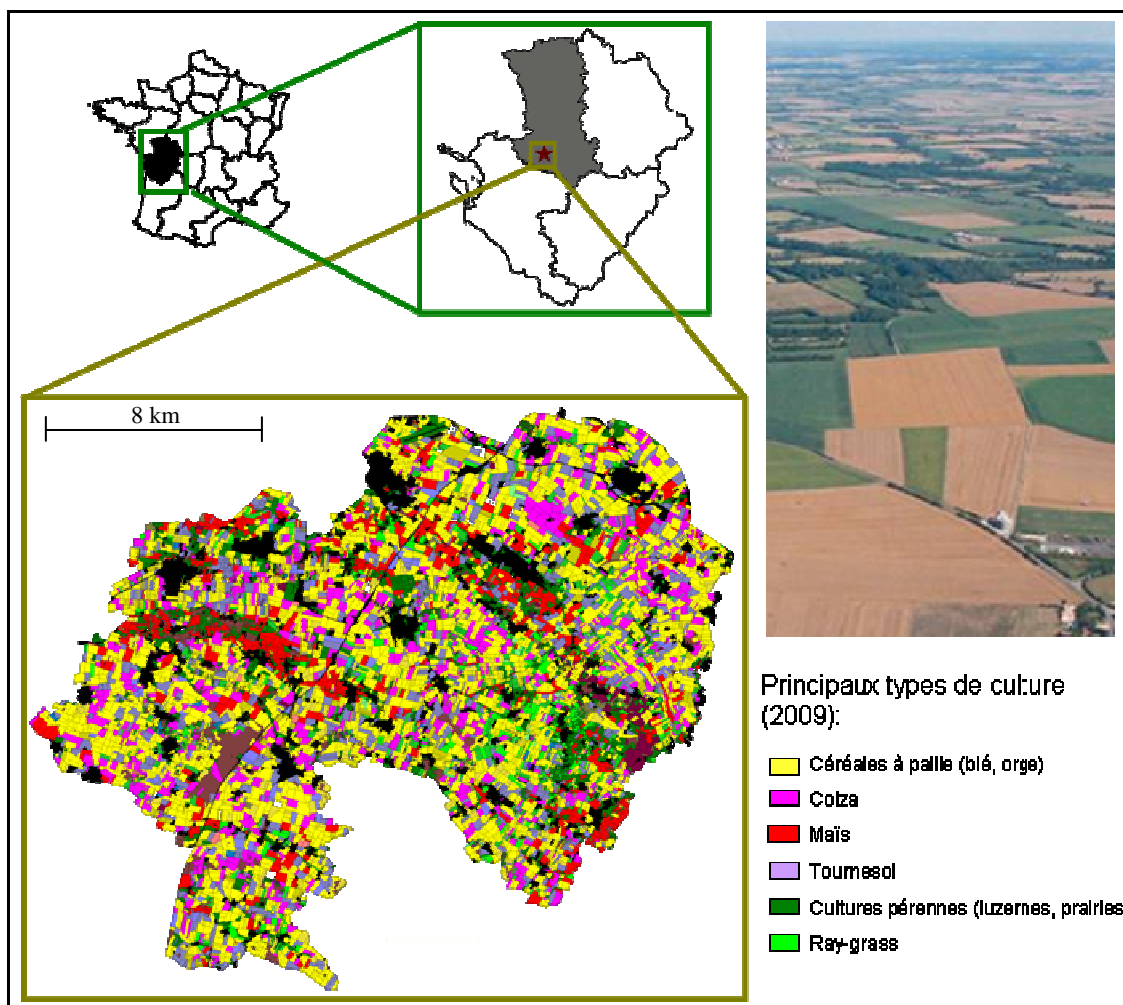


Figure A.9: localisation et structure paysagère de la zone d'étude : la Zone atelier Plaine et Val de Sèvre.





### **A.III. UN TAXON PARTICULIER : LES OISEAUX**

Cette partie traite de la pertinence et des caractéristiques du modèle biologique pour l'étude de la sélection d'habitat dans le contexte du changement global dans un agro-écosystème.

#### **A.III.1. *Les oiseaux : un taxon largement étudié mais approprié***

Les oiseaux sont extrêmement mobiles mais facilement observables et identifiables (Møller et al. 2010). Leur occurrence et leurs comportements font depuis longtemps l'objet d'une attention particulière par les ornithologues et naturalistes (Møller et al. 2010). Les connaissances accumulées sur la biologie des oiseaux sont sans aucun doute les plus approfondies, comparées à n'importe quelle autre classe du règne animal (Møller et al. 2010). Les oiseaux sont certainement le taxon présentant également le plus de données à long terme. Les oiseaux ont largement contribué aux études portant sur la sélection d'habitat (Cody 1985). En effet, de par leur mode de déplacement, leur morphologie, leur physiologie et la large gamme d'habitats qu'ils parcourent, les oiseaux sélectionnent uniquement certains habitats pour leur reproduction, leur alimentation ou leur hivernage (Cody 1985). Les sites de reproduction des oiseaux sont généralement définis comme des localisations fixes dans un environnement dans lequel les œufs peuvent subsister en l'absence des parents (Hansell and Deeming 2002). Cette définition est adaptée aux espèces nidicoles telles que la plupart des oiseaux chanteurs car à la fois les œufs et les poussins ne peuvent survivre à la naissance sans la protection de leurs parents d'où la nécessité d'un nid. En revanche chez les espèces nidifuges telles que les anatidés, seuls les œufs nécessitent la construction d'un nid. Chez ces espèces, la formation des nouveau-nés est relativement bien achevée, d'où une certaine autonomie des jeunes dès la naissance. D'autres espèces encore sont des exceptions à cette définition car ni les œufs ni les poussins ne nécessitent la construction d'un nid fixe. C'est le cas notamment du manchot royal *Aptenodytes patagonicus* et du manchot empereur *Aptenodytes forsteri* (Cody 1985). La construction et la localisation du nid sont donc primordiales chez la plupart des oiseaux et encore davantage chez les espèces nidicoles. Afin de procurer un milieu optimal aux œufs et aux poussins, la sélection du site de nidification, la



forme du nid et les matériaux utilisés sont déterminants (Hansell 2000, Hansell and Deeming 2002). La sélection du site de nidification est soumise à différentes pressions de sélection : la proximité des ressources alimentaires, la disponibilité des matériaux de construction, et surtout l'optimisation des conditions environnementales et la limitation du risque de prédation (Cody 1985, Hansell and Deeming 2002). La localisation et la construction du nid peuvent jouer le rôle de protection contre les prédateurs et d'aide aux parents pour le contrôle de l'environnement (Hansell and Deeming 2002).

Chez les espèces nichant au sol dans des nids souvent rudimentaires, la sélection d'un site de nidification approprié est d'une importance vitale (Limiñana et al. 2006). La structure de la végétation apparaît alors comme déterminante dans le choix d'un site approprié au positionnement du nid. En effet, le taux de recouvrement végétal, la composition spécifique, la densité et la hauteur de la végétation sont avancées comme facteurs primordiaux dans la sélection du site de nidification des espèces nichant au sol en milieu prairial (Bollinger 1995, Helzer and Jelinski 1999). Face aux deux principales pressions de sélection, la prédation et la thermorégulation, les espèces nichant au sol adoptent différentes stratégies. La plupart vont pondre des œufs mimétiques sur sol nu favorisant ainsi une stratégie anti-prédation (visibilité autour du nid) au détriment d'une exposition au soleil (cas de l'Oedicnème criard *Burhinus oedicnemus* dans Solis and De Lope 1995) alors que d'autres favorisent davantage une stratégie anti-insolation en pondant des œufs blancs très détectables par les prédateurs mais réfléchissant davantage les rayons du soleil (Castilla et al. 2007). Certaines espèces utilisent des matériaux particuliers comme des cailloux de couleur claire permettant de réfléchir les rayons du soleil au détriment d'une détectabilité accrue des œufs par les prédateurs (cas du Pluvier siffleur *Charadrius Melodus* dans Mayer et al. 2009). Enfin d'autres espèces choisissent de pondre des œufs mimétiques tout en camouflant le nid dans la végétation favorisant ainsi les deux stratégies. La stratégie adoptée dépend donc des caractéristiques et besoins de l'espèce et de la sélection d'habitat de reproduction qui en découle.

De nombreuses espèces d'oiseaux nichant au sol se reproduisent en milieu agricole. Leur habitat de reproduction est susceptible de subir de fortes variations environnementales liés aux modifications d'usage des sols mais également au changement climatique. Ces espèces présentent donc de forts enjeux de conservation. Pour cette raison, nous avons choisi le Busard cendré *Circus pygargus* comme modèle biologique.



### **A.III.2. Modèle biologique d'étude : Le Busard Cendré *Circus pygargus***

Le Busard cendré *Circus pygargus* est un rapace diurne semi-nidicole (ordre des Accipitriformes) de taille moyenne (43-47 cm de long et 105-120 cm d'envergure; Arroyo et al. 2004). Il existe un dimorphisme sexuel de coloration (femelle brune roussâtre et mâle gris cendré avec des bandes alaires noires, Figure A.10) mais aussi de taille. La femelle est légèrement plus grande que le mâle de par son envergure et de par son poids (masse moyenne  $\pm$  écart-type: 273g  $\pm$  20,  $n = 79$  mâles ; 335g  $\pm$  29,  $n = 119$  femelles ; Millon 2006).



Figure A.10: Busard cendré male (a) et femelle (b: photo © Jean Charennat)

La distribution du Busard cendré est centrée sur l'Europe et l'Ouest de l'Asie (Figure A.11 ; Cramp and Simmons 1980). L'effectif total est estimé à moins de 100 000 couples mais cette espèce n'est pas considérée comme menacée à l'échelle mondiale (Ferguson-Lees and D.A. 2001, International 2004). Cependant, en Europe de l'Ouest, les effectifs paraissent en diminution bien qu'ils soient relativement stables dans les deux plus grandes populations européennes (Espagne et France) depuis les années 80. Le Busard cendré est ainsi classé dans la liste des espèces « A surveiller » (Tucker and Heath 1994) et intégré au livre rouge des espèces menacées en France (Rocamora and Berthelot 1999). L'une des hypothèses expliquant le déclin de l'espèce en Europe de l'Ouest serait la disparition de son milieu originel de nidification (marais et landes) mais aussi l'intensification de la gestion des cultures qui constitueraient leur habitat de reproduction de substitution (Arroyo et al. 1995, Clarke 1996). En effet, aujourd'hui, 70% des couples nicheurs en France sélectionnent les plaines cultivées (Salamolard et al. 2000) où ils nichent au sol principalement dans le blé et l'orge



(70-80%). Son succès de reproduction est donc intimement lié aux pratiques agricoles (la moisson étant une cause importante de mortalité chez les jeunes non volants). On estime que, sans mesures de conservation, 60% des nids placés dans des parcelles cultivées en France et en Espagne peuvent être détruits, rendant ainsi la population non viable en l'absence de protection (Arroyo et al. 2002).

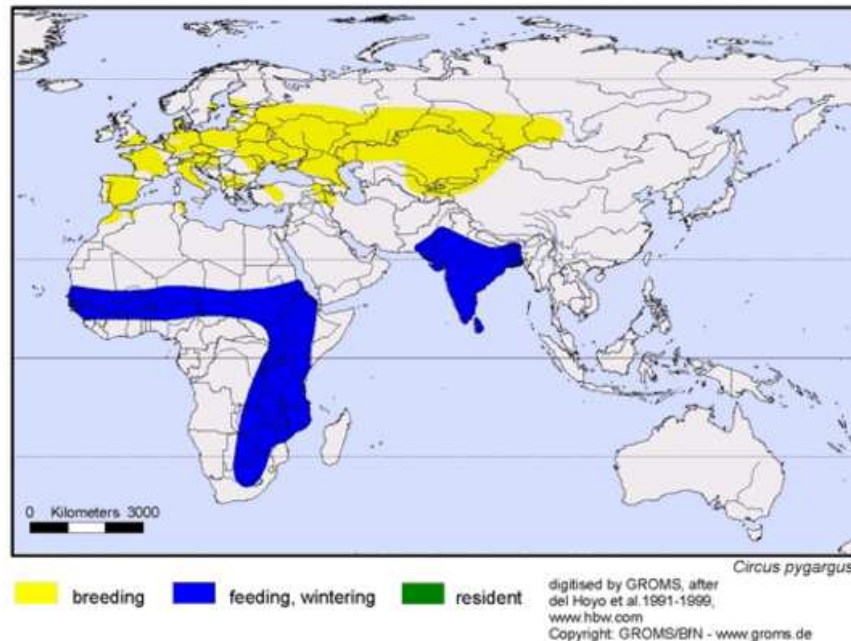


Figure A.11 : distribution mondiale du busard cendré. Les sites de reproduction (en jaune) sont centrés sur l'Asie de l'ouest et surtout sur l'Europe. Les sites d'hivernage (en bleu) sont localisés en Afrique centrale et de l'Ouest mais aussi en Inde.

Migrateur trans-saharien, le Busard cendré ne fréquente ses sites de reproduction d'Europe de l'Ouest que cinq mois par an, entre avril et août, période correspondant également à de nombreux travaux agricoles (Figure A.12). En France, les individus reviennent de leurs sites d'hivernage africain entre début avril et juin mais la majorité est déjà présente sur les sites de reproduction dès la fin du mois de mai. Les dates de ponte présentent de fortes variations latitudinales, en partie dues à des différences dans les dates d'arrivées des oiseaux (Arroyo et al. 2004) mais elles dépendent des conditions climatiques et des abondances de nourriture entre les sites (Salamolard et al. 2000, Arroyo et al. 2004). Dans notre zone d'étude, les dates de ponte s'étalent de fin avril à début juillet (moyenne  $\pm$  SD : 14 mai  $\pm$  11 jours, N = 953 de 1995 à 2011) avec 95% des œufs pondus entre la fin Avril et la mi-Juin (extrêmes : 21 avril – 2 juillet). La taille de ponte moyenne ( $\pm$  SD) des individus nichant dans notre zone d'étude est de  $4.1 \pm 0.99$  œufs (maximum : 8 œufs) mais elle présente de fortes variations inter-annuelles et diminue avec la saison (Arroyo et al. 2004). Les œufs sont d'un



ovale arrondi, lisse mais non brillant de couleur blanche (bleuâtre si juste pondu), rarement marqué avec de fines taches ou des stries rouge-brun (Arroyo et al. 2004). La taille des œufs est constante entre les années :  $41.5 \pm 1.96 \times 33.1 \pm 1.22$  mm (Arroyo et al. 2004). Les œufs sont pondus avec un intervalle moyen de 2 jours puis sont uniquement incubés par la femelle durant 28-29 jours, à partir du 1<sup>er</sup> œuf ou du dernier œuf pondu (Arroyo et al. 2004). Le mâle est chargé de l’approvisionnement en nourriture de la femelle lors de l’incubation et des poussins lors de l’élevage des jeunes (Arroyo et al. 2004). Les jeunes s’envolent après  $32 \pm 4$  jours d’élevage (moyenne  $\pm$  SD). La productivité varie fortement entre sites et années en relation avec l’abondance de la nourriture (Arroyo et al. 2004). Sur notre zone d’étude, la productivité moyenne est de  $3.2 \pm 1.1$  jeunes à l’envol ( $\pm$  SD). Cependant, le succès de reproduction en milieu agricole est fortement influencé par les dates respectives d’envol des jeunes et des activités de récolte des cultures (Arroyo et al. 2004).

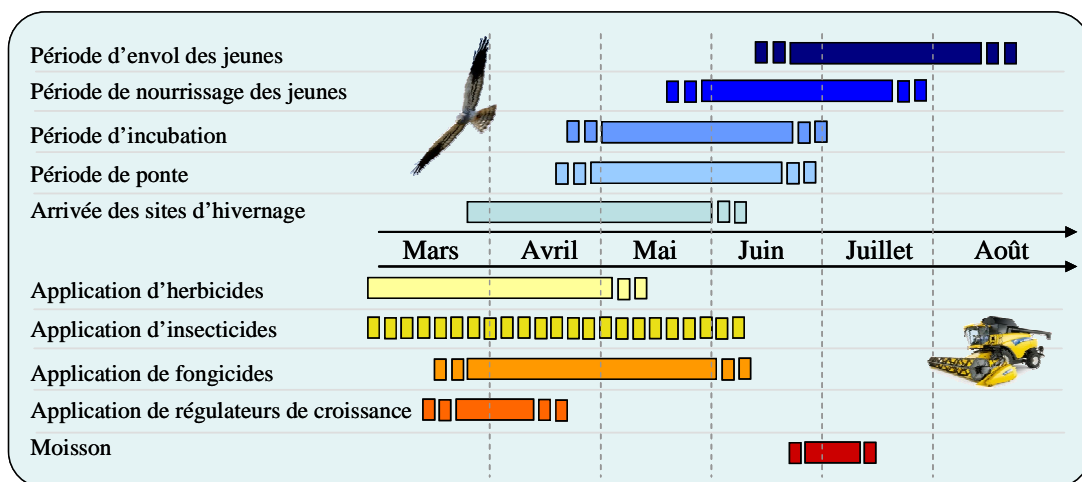


Figure A.12: Cycle de reproduction du busard cendré et planning des interventions agricoles dans les blés. Les aires discontinues indiquent une fréquence moindre du phénomène durant la période considérée.

Lors de la reproduction, l’espèce est considérée comme semi-coloniale : certains nids sont isolés mais la plupart (80-85% en France et en Espagne) forme de petites colonies de 2 à 30 couples (Arroyo et al. 2002, Arroyo et al. 2004). La distance moyenne ( $\pm$  SD) entre nids d’une même colonie (définie comme une agrégation de nids dont la distance minimale entre plus proches voisins n’excède pas 750 m, voir de Cornulier 2005) est de  $155 \pm 137$  m et le nombre moyen ( $\pm$  SD) de nids situé dans une même colonie est de  $5.8 \pm 5.4$  avec un maximum de 21 couples (Arroyo et al. 2004). Globalement, les positions des colonies d’une année à l’autre sont maintenues (Arroyo et al. 2004, Figure A.13) mais les individus



composant ces colonies différent. Néanmoins, la distribution des colonies peut varier de façon inter-annuelle suivant l'abondance de nourriture et le succès de reproduction des colonies lors des années précédentes (Arroyo et al. 2004). Ainsi, les colonies avec des succès de reproduction forts à l'année « n » auront davantage de chance d'accueillir des couples à l'année « n + 1 ». De plus, Arroyo et al. (2004) suggère que le patron temporel d'installation des couples dans une colonie serait influencé par la présence de congénères : les couples tardifs tendraient à s'installer dans des zones déjà occupées et à devenir ainsi coloniaux et non solitaires.

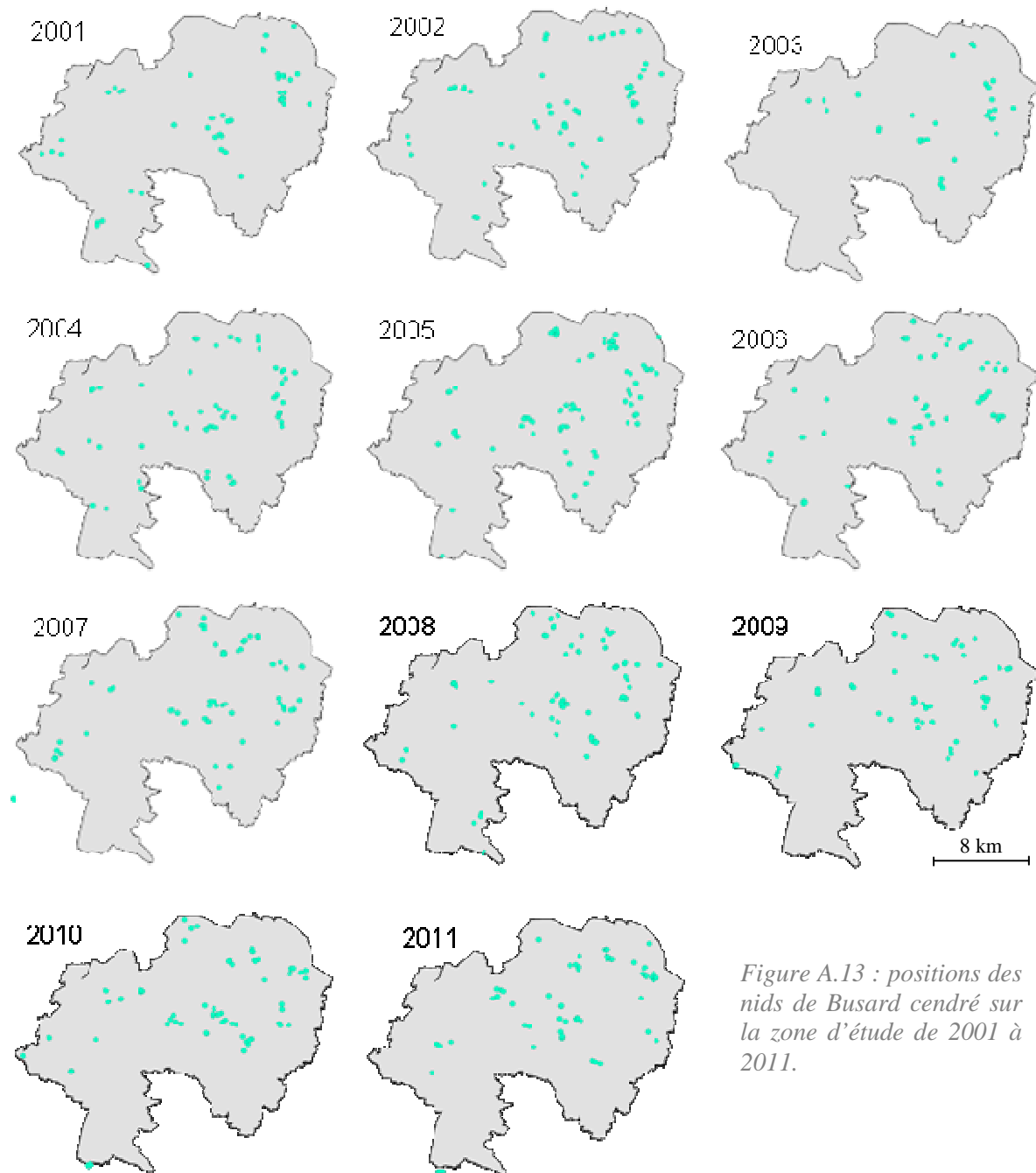


Figure A.13 : positions des nids de Busard cendré sur la zone d'étude de 2001 à 2011.



Le régime alimentaire du Busard cendré sur les sites de reproduction varie de façon annuelle et régionale. Sur notre zone d'étude, l'espèce est spécialisée sur le Campagnol des champs *Microtus arvalis* qui constitue 60 à 90% de son régime alimentaire en biomasse (Salamolard et al. 2000, Arroyo et al. 2004). Ce micromammifère présente sur la zone d'étude des variations cycliques d'abondance de 3 ans (une année « pic » suivie d'une année « crash » puis d'une année « intermédiaire », Figure A.14, Lambin et al. 2006). Cependant l'amplitude de ces cycles a tendance à s'atténuer depuis 2002 (Figure A.14). De nombreuses études ont d'ores et déjà démontré l'influence de ces variations d'abondance de campagnols sur de multiples paramètres de la biologie du Busard Cendré. La date et la taille de ponte (Millon et al. 2008), le succès de reproduction (Millon et al. 2008), le sex ratio de la progéniture (Millon and Bretagnolle 2005), le nombre de couples (Millon and Bretagnolle 2008), l'agrégation des nids (de Cornulier 2005), le recrutement des femelles immatures dans la population reproductrice (Millon and Bretagnolle 2008) ainsi que la durée de la période post- envol des jeunes (Arroyo et al. 2004) sont en effet influencés par l'abondance de campagnols. Ainsi, lors d'une année de forte abondance en campagnols : le nombre de couples nicheurs est important et le taux d'agrégation fort, les femelles de 1<sup>ère</sup> année participent à la reproduction, les dates de ponte sont plus précoces et enfin les tailles de pontes et le succès de reproduction sont plus importants.

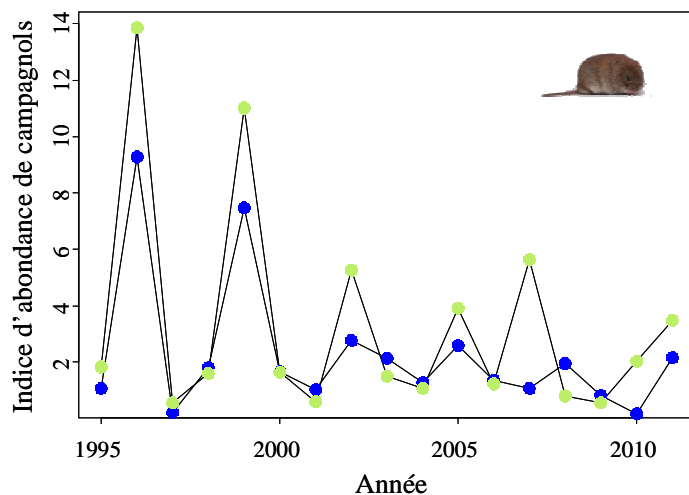


Figure A.14: Evolution des abondances (au printemps ● et en été ●) de campagnols des champs de 1995 à 2011 sur la zone Atelier Plaine et Val de Sèvre

La localisation du site de nidification à l'échelle locale semble être fortement influencée par la hauteur du couvert végétal (Claro 2000, Arroyo et al. 2003, Arroyo et al. 2004, Limiñana et al. 2006) avec une sélection en faveur des hauteurs importantes. Le nid, d'environ 40 cm de diamètre, est relativement rudimentaire (Figure A.15). Il consiste en un monticule aplati de végétations disponibles telles que des brins de roseaux ou de bruyère, des



brindilles, etc. (Arroyo et al. 2004). Le nid est principalement construit par la femelle. Le premier œuf peut être pondu directement sur sol nu ou sur la végétation cassée du nid. Cependant, la femelle peut ajouter des matériaux durant l'incubation et l'élevage des jeunes (Arroyo et al. 2004). De par la localisation des nids dans les cultures et les exigences apparentes de l'espèce vis-à-vis de la hauteur de végétation, il est possible, qu'en plus de l'abondance des campagnols, la disponibilité des hauteurs de végétation des cultures influence la phénologie de reproduction et le succès de reproduction du Busard cendré (à travers des taux de prédation et d'insolation plus importants quand les hauteurs sont faibles). Le Busard cendré et sa fitness pourraient donc être fortement liés à l'habitat de reproduction.



Figure A.15: Nids de Busard cendré localisé dans le blé au stade œuf (a) et au stade poussin (b).

En termes de conservation, il apparaît primordial de comprendre le choix du site de nidification du Busard cendré et de l'ensemble des espèces agricoles nichant au sol car la structure de la végétation dans laquelle ils nichent est déterminée par les activités anthropiques et les variations climatiques. La sélection de l'habitat par ces espèces est fortement soumise à l'influence des variations spatiales et temporelles dues au changement





---

global de l'habitat au sens large (physique, biologique et social). L'étude de la sélection d'habitat de reproduction du Busard cendré peut nous permettre de mieux comprendre la réponse de l'espèce face aux variations de son habitat et d'appréhender son avenir en milieu agricole dans le contexte du changement global.



## **A.IV. OBJECTIFS ET STRUCTURE DE LA THESE**

Au cours de cette introduction générale, nous avons vu que les organismes sélectionnent leur habitat à différentes échelles spatiales selon l'utilisation particulière de celui-ci (pour la reproduction, l'alimentation, etc.) et vis-à-vis de trois composantes qui interagissent : les caractéristiques physiques, biologiques et sociales de l'habitat. Ces trois composantes sont toutes susceptibles d'être affectées par le changement global actuel. Ce dernier est d'autant plus intense dans les milieux fortement anthropisés, tels que les milieux agricoles qui subissent à la fois les changements du climat, de l'utilisation des sols et une surexploitation des ressources. Les espèces inféodées au milieu agricole, comme certains oiseaux nichant au sol, sont particulièrement exposées à des modifications ponctuelles ou à long terme de leur habitat pouvant avoir des conséquences sur leur fitness. Au vu de ces éléments, l'étude de la sélection d'habitat de reproduction des espèces agricoles nichant au sol apparaît comme primordiale pour comprendre l'effet des changements environnementaux en cours et à venir et à en prédire les effets sur les populations.

Les objectifs globaux de cette thèse sont de comprendre les facteurs principaux qui dirigent le choix du site de nidification et plus particulièrement le choix de la hauteur de végétation au nid du Busard cendré en milieu agricole intensif par une approche multi-échelle. La sélection d'habitat est en effet étudiée à l'échelle du nid, de la colonie et du paysage de manière intra- et inter-annuelle. Les causes de ces choix mais également les effets sur la fitness des individus sont également abordées. De plus, les conséquences des variations temporelles et/ou spatiales (potentiellement dues au changement global) de la disponibilité des hauteurs de végétation, des ressources alimentaires et des densités de conspecifics sur la sélection du site de nidification sont investiguées. A la lumière des mécanismes et des premières tendances à long terme de la sélection d'habitat mis en évidence dans le volet « principaux résultats » de cette thèse, une réflexion sur l'avenir et la conservation du Busard cendré en milieu agricole intensif dans le contexte du changement global est développée dans le dernier volet du manuscrit.

Plusieurs champs théoriques, depuis l'écologie évolutive jusqu'à l'écologie du paysage, ainsi que l'écologie comportementale, ont été explorés, en optant le plus souvent pour une approche mécaniste. Les résultats obtenus au cours de la thèse s'articulent autour de quatre parties (chapitres I à IV du volet « principaux résultats ») Ces parties sont constituées de



quatre articles soumis ou en préparation accompagnés de résumés introductifs replaçant les études dans le cadre plus général de la thèse.

La première partie vise à comprendre le rôle, le choix et l'utilisation de la hauteur de végétation par les oiseaux nichant au sol. Il s'agit plus précisément d'évaluer l'importance relative des processus sous-jacents à la sélection de hauteur de végétation au nid, la prédation et l'insolation des œufs et des poussins, au cours d'une saison de reproduction. L'importance de ces deux pressions de sélection est en effet susceptible d'être modifiée par le changement global : la communauté de prédateurs peut évoluer et le risque d'insolation peut augmenter. Cette étude se base sur une expérimentation *in natura* effectuée durant deux saisons de reproduction. La stratégie de reproduction du Busard cendré a été utilisée comme guide conceptuel pour la mise en place du design expérimental.

Après avoir identifié l'importance relative des processus clés déterminant la sélection d'une hauteur de végétation au nid, une deuxième partie aborde les patrons globaux de sélection de hauteur au nid du Busard cendré ainsi que les variations temporelles (intra et inter-annuelles) de cette sélection et leurs conséquences sur la fitness. L'influence des variations des trois composantes de l'habitat à travers la phénologie de la végétation, l'abondance de proies et la densité de congénères est prise en compte. L'étude se base sur 15 ans de données permettant ainsi une exploration des tendances dans la sélection potentiellement imputables au changement global. Ce chapitre fait appel à différents domaines scientifiques notamment aux sciences agronomiques de par la modélisation de la croissance des cultures.

La prise en compte de l'aspect social d'une espèce semi-coloniale telle que le Busard cendré étant primordial pour les études de sélection d'habitat et pour la mise en place de mesures de conservation adéquates, nous nous sommes intéressés dans une troisième partie aux patrons temporels d'installation des individus au sein d'une colonie. L'impact de l'aspect social (présence de congénères) sur le choix d'une hauteur de végétation (sur la qualité d'un patch) est mis en avant. Le choix par l'utilisation de l'information personnelle (basé sur la qualité intrinsèque des patches) ou publique (basée sur la présence de congénères) est donc ici contrasté. L'étude s'appuie sur trois années de récolte de données à l'intérieur des principales colonies de Busard cendré situées sur la plaine agricole sud-niortaise.

Enfin, dans une quatrième et dernière partie, nous souhaitons, dans la continuité des seconde et troisième parties, aborder les dimensions temporelle et surtout spatiale de la distribution des habitats potentiellement favorables à la nidification du Busard cendré. Nous



---

avons donc étudié la position des nids (et donc des colonies) à plusieurs échelles spatiales selon la répartition dans l'espace d'un indice de précocité du blé (proxy de la hauteur de végétation en début de saison). Une approche novatrice combinant données satellites et données sur le terrain, récoltées sur 10 ans a ici été utilisée.



## B. Principaux résultats





Les résultats seront abordés sous formes d'articles pouvant être soit soumis (Articles 1 & 2), soit en préparation (Articles 3 et 4). Ils sont composés de quatre chapitres qui correspondent aux articles cités précédemment. Chaque chapitre est composé d'un résumé détaillé de l'article (en français) et de l'article en lui-même (en anglais).

Les articles sont listés ci-dessous :

- **Article 1:** Vegetation height and egg coloration differentially affect predation rate and overheating risk: an experimental test mimicking a ground-nesting bird
  
- **Article 2:** Where and when to breed do matter: temporal variation in selection of vegetation height at the nest for a ground-nesting raptor in farming habitats
  
- **Article 3:** Is there a balance between physical and social cues for nesting habitat choice in a facultative colonial breeder?
  
- **Article 4:** Breeding habitat selection of a farmland ground-nesting bird: an approach at multiple spatio-temporal scales using remote sensing.



## **B.I. PROCESSUS SOUS-JACENTS A LA SELECTION D'UN SITE DE NIDIFICATION CHEZ LE BUSARD CENDRE**

### **B.I.1. Résumé du chapitre**

Dans cette étude, nous souhaitons comprendre les processus sous-jacents à la sélection d'une certaine hauteur de végétation chez le Busard cendré et plus généralement chez les oiseaux nichant au sol. La littérature actuelle met en avant deux principales pressions de sélection : le risque d'insolation et surtout le risque de prédation des œufs et des poussins. La couleur des œufs interagit avec les deux risques mais de manière souvent opposé : un œuf blanc réfléchit la lumière (diminuant ainsi le risque d'insolation) mais est plus détectable par les prédateurs et l'inverse est attendu pour un œuf de couleur sombre. En outre, le rôle de la structure de la végétation (hauteur, densité, composition spécifique) dans la protection des nichées face à ces deux risques est largement mis en avant, notamment chez les espèces prairiales. Cependant, jusqu'ici, la plupart des études traitaient seulement d'une des deux pressions en ne faisant que mentionner l'autre. En effet, la hauteur de la végétation jouant un double rôle, il est difficile de distinguer les forces respectives de ces pressions dans la sélection, par les oiseaux, de paramètres de la structure de végétation tels que la hauteur du couvert.

L'objectif final de notre étude était donc d'aboutir à une formalisation conceptuelle de l'importance relative des deux principales pressions de sélection au cours d'une saison de reproduction. Nous avons donc utilisé, de manière expérimentale, la hauteur de végétation, l'augmentation de la radiation solaire (augmentant le risque d'insolation) mais aussi la couleur des œufs afin de manipuler différenciellement les deux risques. Il est important de préciser que notre étude ne visait pas à mimer les conditions réelles rencontrées par des œufs mais à estimer globalement l'importance relative des deux pressions suivant la hauteur de la végétation et la période de la saison de reproduction. Les méthodes et les résultats sont présentés et discutés en détail dans la partie rédigée en anglais. Nous nous attacherons donc ici à faire un résumé succinct de ceux-ci.

Une approche expérimentale *in natura* basée sur la stratégie de nidification du Busard cendré (nichant principalement dans le blé) a été utilisée durant deux saisons de reproduction. D'une part, nous avons exposé des œufs factices en plâtre de couleur blanche dans une large gamme de hauteurs de blé (35 - 115 cm) afin d'évaluer le risque de prédation selon la hauteur





du couvert (Figure B.1.a). Afin d'estimer la détectabilité des œufs par les prédateurs selon leur coloration et selon la hauteur du couvert, des œufs de couleur verte (mimétique dans le blé) ont également été exposés dans une gamme restreinte de hauteurs (qui maximise le risque de prédation : 35-65 cm). D'autre part, nous avons placé des capteurs de température (Figure B.1.b) dans la large gamme de hauteur afin de mesurer les conditions microclimatiques induites par différentes hauteurs de blé. Un risque d'insolation a été calculé selon la durée d'exposition (15min) au-dessus d'une certaine température (41°C, température létale des œufs). Les deux expériences ont été répétées 3 fois durant chaque saison de reproduction afin d'évaluer l'évolution temporelle des risques.

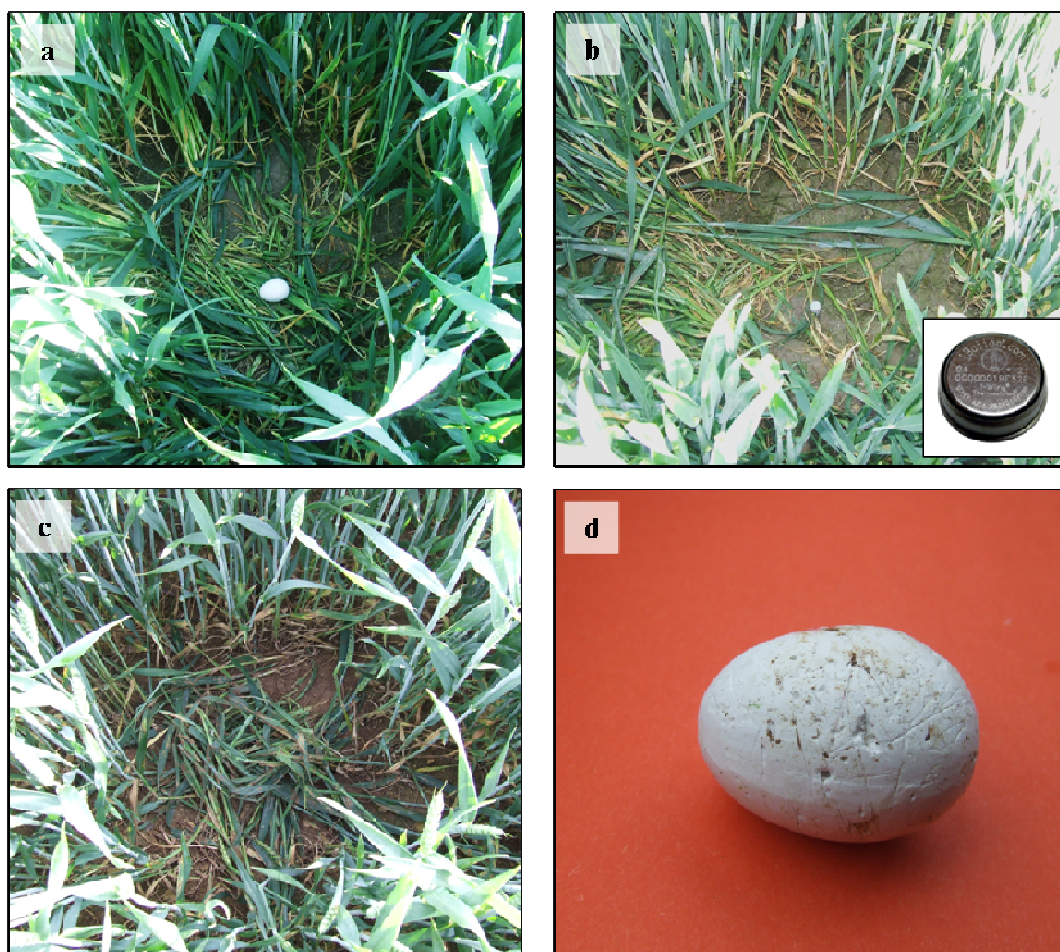


Figure B.1: Photographies illustrant un faux nid avec un œuf blanc factice (a), un faux nid avec un enregistreur de température (Thermochron® iButton) (b), un faux nid dans lequel l'œuf a disparu (c) et les traces de prédation d'un corvidé sur un œuf en plâtre (d)

Les résultats obtenus montrent que le risque de prédation diminue avec la hauteur de végétation et ce d'autant plus rapidement que les œufs sont mimétiques. La forte relation négative entre le risque de prédation et la hauteur du couvert suggère que la communauté de



prédateurs sur notre zone d'étude est dominée par les oiseaux (figure B.1.c & d). Ce risque est constant, pour une hauteur de couvert donnée, le long d'une saison de reproduction quelque soit la couleur de l'œuf, suggérant que la communauté et le comportement alimentaire des prédateurs ne varient pas durant une même saison. Le risque d'insolation diminue également avec la hauteur de végétation mais augmente, pour une hauteur de couvert donnée, avec l'avancement de la saison de reproduction. L'augmentation de ce risque le long de la saison est due à l'augmentation de la radiation solaire au cours du printemps à nos latitudes. Les conditions microclimatiques sont donc davantage favorables dans des hauteurs de couvert importants et en début de saison.

Le risque de prédation étant constant et le risque d'insolation augmentant avec l'avancement de la saison, il est concevable que, pour une hauteur donnée, l'importance relative de ces risques s'inverse à un moment donné dans la saison de reproduction. En milieu tempéré, les oiseaux nichant au sol sont donc soumis à deux contraintes, dont l'importance relative change au cours d'une saison de reproduction. Ces changements doivent être susceptibles d'affecter les patrons de sélection de site de nidification observés mais également l'effort de protection du nid par les parents (durées et fréquences de l'absence des parents). Le choix final d'une hauteur de végétation dépend donc de la date de ponte de l'espèce et de l'individu mais aussi des potentiels comportements alternatifs aidant à la protection de leur nichée.

Notre modèle d'étude, le Busard cendré, fait face à des hauteurs de céréales qui augmentent considérablement le long de la saison de reproduction (en moyenne de 30-40 cm début avril à 80-90 cm fin juin). Pourtant, notre étude suggère que le Busard doit pondre dans des hauteurs de végétation importantes tout au long de la saison afin de protéger ses œufs blancs du risque de prédation (mais aussi du risque d'insolation en fin de saison). Par conséquent, en début de saison, les individus précoces seraient soumis à une forte pression les obligeant à être très sélectifs sur la hauteur. Cette pression se relâche ensuite au cours de la saison, grâce à la croissance des céréales. Cet article pose donc les bases du chapitre suivant en nous permettant de conceptualiser le patron de sélection du busard cendré vis-à-vis de la hauteur de végétation au nid au cours d'une saison de reproduction.

Des variations inter-annuelles des risques de prédation et d'insolation mais aussi des hauteurs disponibles ont également été mises en évidence. Ces observations suggèrent que, dans le contexte du changement global, l'importance des deux pressions de sélection soit susceptible d'être bouleversée. En effet, le changement global pourrait affecter la composition



des communautés de prédateurs, ainsi que leurs comportements, tandis que le changement climatique pourrait augmenter les températures ambiantes et donc le risque d'insolation. D'autre part, la hauteur et la précocité des blés étant fortement dépendantes des conditions climatiques et des pratiques agricoles, les hauteurs disponibles pourraient être altérées suite au changement global. En réponse ces potentiels changements, les Busards cendrés devraient adapter leur stratégie de nidification. Dans le cas contraire, la persistance des populations en milieu agricole pourrait être menacée.



## ***B.I.2.     Article 1***

**Vegetation height and egg coloration differentially affect predation rate and overheating risk: an experimental test mimicking a ground-nesting bird.**

H. GILLIS\*, B. GAUFFRE, R. HUOT and V. BRETAGNOLLE

Centre d'Etudes Biologiques de Chizé, CNRS-UPR 1934 Villiers-en-Bois, France

\* Corresponding author: Hanneke Gillis:

Email address: [gillis@cebc.cnrs.fr](mailto:gillis@cebc.cnrs.fr); [hanneke.gillis@yahoo.fr](mailto:hanneke.gillis@yahoo.fr)

Soumis à: **The Canadian Journal of Zoology**



### ***Abstract***

Avian eggs need to be laid in protected environments to develop and survive. Nest predation is known as the main cause of breeding failure but nest microclimate conditions are also important for embryo development. These two selective pressures are particularly marked in ground-nesting birds. Vegetation height has been showed to be a critical factor in ground-nesting birds since it can counteract predation and overheating simultaneously. It is therefore difficult to disentangle the respective influences of these risks on selection of a particular nest vegetation height. To develop a conceptual framework for understanding and predicting their relative effects during a breeding season, we used vegetation height to manipulate differentially these two risks. We therefore exposed artificial nests to a wide range of vegetation heights, replicated the experimental tests during spring, and manipulated egg color to estimate predation risk. We confirmed that tall vegetation is relevant to protect unattended eggs against both risks. While predation risk is stable for a given vegetation height, overheating risk presents inter- and intra-seasonal variations. Therefore, over a breeding season, for a given vegetation height, the respective strengths of the two risks are unbalanced and depends on egg coloration. The breeding strategy of ground nesting birds should thus have been shaped by both selective pressures, but the ultimate choice may depend on the species-specific laying dates and alternative behavioral strategies helping to protect the clutch.



## ***Introduction***

Terrestrial vertebrates have developed two main strategies to ensure embryo development: embryos of viviparous species develop inside the body of the mother, guaranteeing protection from hostile environments, while in oviparous species, females lay eggs. In that latter case, while females avoid the costs of embryonic development inside their body, in return eggs must be laid in environments safe with regard to their development. Two main environmental constraints have been identified for eggs: abiotic (mainly related to physical factors such as temperature, salinity and humidity) and biotic selective pressures (predation, parasitism; Holway 1991, Martin 2001). Though predation is considered the most important cause of breeding failure in birds (Ricklefs and Institution 1969), birds are endotherm organisms and therefore their eggs also require an appropriate physical environment that ensures optimal temperature conditions (Walsberg 1985, Webb 1987, Ghalambor and Martin 2002, Lusk et al. 2003). Egg hypothermia may lead to developmental abnormalities of the embryo, whereas hyperthermia may be responsible for embryo malformations or even death (Bakken et al. 1978, Conway and Martin 2000).

Birds have therefore evolved nesting strategies that respond to these selective pressures: to protect eggs from predation, they nest in areas which restrain nest accessibility to predators (Martin and Roper 1988, Martin 1995, Dion et al. 2000), decrease (Tinbergen et al. 1967, Dion et al. 2000) or increase (i.e. colonies) conspecific nest densities, reduce nest detection by using cryptic nests (i.e. nest concealment by vegetation structure : Schieck and Hannon 1993, Dion et al. 2000), lay mimetic eggs (Solis and De Lope 1995, Avilés et al. 2006), use active nest defense or mobbing (Cresswell 1997, Arroyo et al. 2001), reduce clutch size (Perrins 1977, Lundberg 1985, Gregoire et al. 2003), or maintain constant presence at nest (Kilner 2006). To avoid extreme temperatures affecting their eggs, birds have also developed various strategies, including selecting nest sites that reduce heat stress (e.g. structural vegetation cover; Colwell 1992, Lusk et al. 2003, Wells and Fuhlendorf 2005), building nests that reduce temperature variations either through particular shapes (Ar and Sidis 2002, Deeming 2002) or nest materials (e.g. Howey et al. 1984, Mayer et al. 2009) and keeping permanent presence at nest (Kilner 2006). Additionally, the white ancestral color of eggs (Kilner 2006) could reduce overheating by reflecting solar radiation (Castilla et al. 2007). However, while concealment and parent presence at nest protect eggs from both predation and overheating, egg coloration interacts with both risks but in opposite ways (Bakken et al. 1978): mimetic colored eggs reduce predation risk (e.g. Weidinger 2001) but



may increase overheating risk in comparison to white eggs for which the reverse consequences are expected.

Compared to the more commonly observed tree-nesting and cavity-nesting birds, ground-nesting species face higher risks of predation (Ricklefs and Institution 1969) and overheating (Deeming 2002) because they usually build rudimentary nests at exposed sites which makes unattended eggs more vulnerable (Bakken et al. 1978): Vegetation height has been identified as a critical determinant in the nesting strategy of ground-nesting birds (Helzer and Jelinski 1999), e.g. those breeding in steppe or agricultural landscapes. Since nesting in tall vegetation (thus increasing nest concealment) has the potential to counteract both predation and overheating risks (Colwell 1992, Lusk et al. 2003), it is therefore difficult to disentangle the respective influences of these two risks on micro-habitat selection, and ultimately, the evolutionary forces that have shaped particular breeding strategies. As most ground-nesting birds lay mimetic eggs (Magige et al. 2008), one may conclude that predation is the most important evolutionary pressure that has shaped ground-bird nesting strategy. However, some ground-nesting bird species lay white eggs (e.g. many Anatidae), suggesting that, in some cases, overheating risk may have been important in shaping breeding strategies.

Many studies have attempted to estimate either predation risk or overheating risk using artificial nests and eggs. In contrast, here we use an experimental design to identify the respective strength of the two selective pressures, predation and overheating, on egg survival over time in order to propose a conceptual scheme that embodies the relative importance of these pressures across a breeding season. Therefore, we used vegetation growth during spring as a way to manipulate differentially the two risks. In temperate ecosystems, vegetation height and solar azimuth both gradually increase with season (i.e. spring). Eggs on the ground should thus experience different durations of sun exposure depending on vegetation height relatively to calendar date. By replicating along the breeding season an experiment in which vegetation height was controlled and almost identical in range between replicates, we exposed artificial nests to a constant gradient of predation risk (i.e. varying only with vegetation height) while the overheating risk increased (i.e. with increasing solar azimuths). In addition, we manipulated egg color to estimate predation risk. We used the breeding strategy of the Montagu's harrier *Circus pygargus* as a conceptual guide for our experimental design. This species lays white eggs mainly in wheat crops (Arroyo et al. 2004) and performs only female brooding. Along a gradient of vegetation height over the course of two complete breeding seasons, predation rate of artificial nests was recorded with white or mimetic dummy eggs



while temperature of artificial nests was recorded with data loggers. We first checked that (1) egg predation and overheating risk decrease with vegetation height, and then predicted that (2) mimetic eggs will be less predated than white ones, and that (3) predation risk at a given vegetation height will be constant over a breeding season while overheating risk will increase.

## *Material & Methods*

### Experimental design

Experiments were undertaken in an intensively managed farmland landscape located in the region of Deux-Sèvres (46°11'N, 0°28'W), central-western France, during the springs of 2009 and 2010 (see Millon and Bretagnolle 2008 for a full description of study site). In both years, we performed three sessions (for each experiment, i.e. overheating and predation) from end of April to end of June to encompass the complete breeding season and a complete range of solar azimuth angles and crop heights. Experimental plots were chosen according to their vegetation height and their crop type (only winter cereals). Vegetation heights were classed in 10 cm categories and ranged from 30 - 40 cm to 120 - 130 cm. For each session, we tried to maximize the range of vegetation heights at experimental nests, depending on seasonal growth of wheat which affected height availability. Predation and overheating experiments were performed on different dummy nests. A total of 123 and 108 nests were set for the predation and the overheating experiments, respectively (see Appendix A).

### *Artificial nests*

Artificial nests were standardized: they were made by trampling vegetation and creating a 50 cm-diameter "hole" in the crop, were settled at least 20 m away from the border of the field, 2 m from tractor trails to avoid mammalian predators that favor tracks, at least 200 m away from any building (village, farm), and at least 100 m from woods and hedgerows to limit variations in predator community and minimize tree shadow on recorded temperatures.

### *Predation experiment*

In each artificial nest, we placed one white plaster egg (plaster eggs were obtained by using an infertile harrier egg to shape the mold). Eggs were marked with a small symbol (applied with pencil) facing towards the soil to detect whether the dummy egg was





manipulated by a predator. Eggs were exposed for 7 days and checked 24 h after installation and subsequently every 48 h. Regular nest visits were performed to avoid several predation events on the same nest. Installation and visits were performed at dusk to avoid visual detection by bird predators and boots were worn to prevent spread of human odors for mammalian predators. Nests were considered predated if the egg had disappeared, showed predation marks made by teeth, beaks or claws, or had been manipulated (as assessed by the mark on the egg), and the trial was stopped for this particular nest. If “predated” eggs were still in the nest, we tried to identify the predator type (bird *versus* mammal) using predation marks left on the plaster egg.

In 2009, a single nest with a white egg was placed in each selected plot (N=51). In 2010, to assess differences in egg detectability and predation in relation to egg coloration, we also placed 29 second artificial nests with one mimetic plaster egg (painted in khaki green to mimic wheat color) among the 72 experimental plots chosen for white dummy eggs. The color of mimetic eggs was chosen in relation to eggs of the little bustard *Tetrax tetrax*, a ground nesting species also breeding on the study area which lay eggs of approximately the same size as our plaster eggs. These additional nests were set at least 50m away from the “white egg” nests and were only placed in low vegetation categories (from 30-40 to 60-70 cm) in order to maximize predation risk (see Appendix A1).

#### *Overheating test*

To obtain a proxy of microclimate conditions (i.e. temperatures) in different vegetation heights, we used disc-shape temperature data loggers (DS1921G Thermochron<sup>®</sup> iButton, Sunnyvale, CA, U.S.) programmed to record temperature every 3 minutes with 0.5 °C precision. For each session, loggers were mounted on a nail and stuck in the ground of an empty artificial nest (same plots but different nests than the ones used in predation experiment) during four days. Loggers were not in direct contact with soil but on a small layer of trampled wheat. Tests were performed when weather was sunny (and weather forecast were such for the next four days), i.e. when overheating risk is maximal (Appendix A2). To evaluate the effect of extreme microclimate conditions, we only used data of the warmest 24 hours among the four days recording. We choose to determine a temperature and exposure duration value to estimate a threshold over which nest microclimate conditions became unfavorable for nesting and thus when overheating risk could be considered. Therefore, we considered that a logger recording temperatures  $\geq 41^{\circ}\text{C}$  for  $\geq 15$  minutes (5 successive



records) would reach this threshold. These values (i.e. temperature and duration) were chosen because in most species, egg exposition to 41°C for few minutes is lethal (see Conway and Martin 2000 for examples of off-bout durations in several species, Webb 1987 and Magige et al. 2008 for lethal egg temperature). Additionally, to improve robustness of the analysis, we also tested other threshold temperatures and durations. Hence, we explored exposure time (daily cumulative number of records) at temperatures thresholds from 30 to 55°C on the session involving the widest range of vegetation height categories (second session in 2010).

For each session, we replaced julian date by solar radiation because we assumed that the latter should better explain differences in overheating probability and unveil potential intra-seasonal variations. We recovered a solar radiation index to account for the increase of solar azimuth with season and therefore radiation. The global solar radiation at ground level (in kWh/m<sup>2</sup>/day) of Poitiers (i.e. the closest location available, c.50 km away from study plots) was thus calculated with the software CalSol (INES, Le Bourget du Lac, France) for the warmest day of each session.

### Statistical analyses

Statistical analyses were performed with R (version 2.12.1, R Development Core Team, 2010). We used Generalized Linear Models (GLM) to analyze the effect of vegetation height on white egg predation and overheating probabilities. A Generalized Linear Mixed Model (GLMM) was used to test the effect of egg color on predation probability. We indeed accounted for the fact that the two nests (with different egg colors) were in the same field. Therefore field identity was treated as a random effect in that latter case. We tested *a priori* hypotheses and therefore ran complete models without performing model selection.

In the first analysis, “White egg predation”, the dependent variable, was coded as a binomial variable (predation was considered after 7 days exposure). Independent variables considered in the model (with logit link function) were vegetation height (in cm) and session date (in julian days, i.e. 1 = January 1<sup>st</sup>) as continuous variables, and year as a two-level factor (2009/2010). In the second analysis, differences in predation rate according to egg color was investigated by including only plots with both egg colors in the model (N = 29). Apart from egg coloration (a two-level factor: white/green), fixed effects included in the model were those found to have significant effects in the first analysis (i.e. “white egg predation” analysis).



Finally, to analyze overheating data, the temperature values were converted into a binomial variable, “overheating”, coded as 1 if the logger recorded temperatures  $\geq 41^{\circ}\text{C}$  for  $\geq 15$  minutes, 0 otherwise. Vegetation height and the index of solar radiation, as continuous variables and year as a two-level factor were the independent variables.

In each analysis, we included all simple effects as well as second order interaction terms involving vegetation height to test our hypotheses.

## Results

### Predation rate

Of the 123 artificial nests with white eggs, 67 were predated (54.5 %): 45.1% ( $n = 23$ ) in 2009 and 61.1% ( $n = 44$ ) in 2010. Among these, 38 nests (56.7 %; 16 in 2009, 22 in 2010) were retrieved empty and causes of predation were therefore not identifiable. In the remaining 29 “predated” nests, the eggs were still present and predator could be identified in 21 of these: 18 (85.7 %, 4 in 2009 and 14 in 2010) were predated by corvids and 3 by mammals (14.3 %, none in 2009 and 3 in only tall vegetation in 2010). Given the high number of unknown predators, predated nests were pooled for subsequent statistical analyses regardless of the predator.

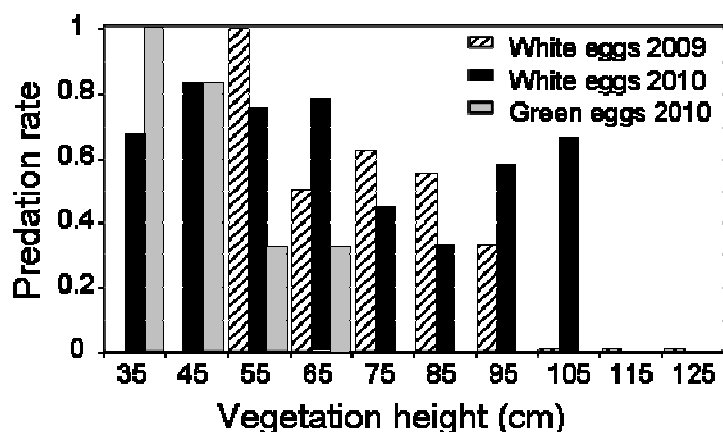


Figure 1: Predation rates as a function of vegetation height. Hatched bars represent predation rates of white eggs in 2009, black bars, predation rates of white eggs in 2010 and grey bars, predation rates of green mimetic eggs (2010). For white eggs in 2009, predation rates in very high vegetation categories (from 105 to 125 cm) were null. Otherwise, absence of bars traduces absence of sampling in corresponding vegetation height.

White egg predation rate was affected by vegetation height, year and their interaction (Tab. 1). It decreased significantly with vegetation height in both years but in a weaker way in 2010, as exemplified by the significant interaction between these two factors (Tab. 1, Fig. 1). However, this year difference might be due to differences in tested vegetation heights between years. We thus performed a GLM (with an identity link) to investigate temporal differences in tested heights by examining the effects of year, session and their interaction.



Tested vegetation heights were indeed higher in 2009 than in 2010 (mean  $\pm$  standard deviation:  $87 \pm 19$  cm in 2009 and  $71 \pm 19$  cm in 2010;  $F_{1, 121} = 12.9$ ,  $p < 0.001$ ), and they logically increase with session (i.e. with season,  $F_{1, 121} = 18.36$ ,  $p < 0.001$ ; no significant interaction was found).

Table 1: GLM investigating predation rate of white eggs ( $N = 123$ ). Estimated coefficients (Estimate), standard error around estimation (SE), statistic  $z$  and  $P$ -values are presented. “2009” is considered as the reference year.

variable	Estimate	SE	z	P
Intercept (2009)	0.2	0.36	0.56	0.57
Vegetation height	-1.64	0.46	-3.59	<0.001***
Year (2010)	0.07	0.44	0.13	0.90
Session	-0.05	0.21	-0.22	0.82
Vegetation height $\times$ Year (2010)	1.24	0.55	2.27	0.02*
Vegetation height $\times$ session	0.36	0.26	1.35	0.18

Egg color also affected the probability of a nest being predated at low vegetation (30-70 cm). 22 of 29 nests with white eggs (76%) were predated compared to only 15 of 29 mimetic eggs (46.7%). Since, “egg color” experiment was only performed in 2010, year was not included in the model. Only vegetation height, egg coloration and their interaction were therefore tested. At low vegetation, green eggs were thus less predated than white ones (Tab. 2). Predation probability of white eggs remained high while predation probability decreased with vegetation height for mimetic green eggs, as shown by a significant interaction between egg color and vegetation height (Tab 2, Fig. 1 & 3). For instance, at vegetation height of 60-70 cm, predation risk of mimetic eggs was below 20% while it was over 80% for white eggs (Fig. 3).

Table 2: Generalized linear mixed model investigating the effect of egg color on predation rate in low vegetation categories ( $N = 58$ ). Estimated coefficients (Estimate), standard error around estimation (SE), statistic  $z$  and  $P$ -values are presented. The plot identity was treated as a random effect. “White” is considered as the reference color.

variable	Estimate	SE	z	P
Intercept (white)	5.89	2.09	2.81	0.005**
Vegetation height	0.02	2.23	0.01	0.99
Color (green)	-5.13	2.12	-2.42	0.01*
Vegetation height $\times$ Color (green)	-5.30	2.562	-2.10	0.03*



### Overheating risk

As expected, there were differences in temperatures between low and tall vegetation (Fig. 2a). Temperatures higher than 50°C were recorded in 30-40 cm vegetation whereas at 100-110 cm vegetation, the maximal recorded temperature was only 35°C (Fig. 2a). Overheating risk (i.e. unfavorable nest microclimate conditions) appeared much stronger in 2010 than in 2009, as revealed statistically by the difference in intercept in the year effect (Tab. 3). But for both years, the risk obviously increased with solar radiation (Tab. 3). However, in 2009, vegetation height did not affect recorded temperatures, while in contrast, in 2010, overheating risk decreased significantly with vegetation height (Tab. 3). Here again, we suspect differences in tested vegetation heights between years to be the main reason of difference of overheating risk between years (see section “predation rate” in results).

Table 3: GLMM investigating overheating risk ( $N = 108$ ). Estimated coefficients (Estimate), standard error around estimation (SE), statistic  $z$  and  $P$ -values ( $P$ ) are presented. “2009” is considered as the reference year.

variable	Estimate	SE	z	P
Intercept (2009)	-2.87	0.78	-3.67	<0.001***
Vegetation height	0.35	0.75	0.47	0.64
Solar radiation	1.94	0.52	3.68	<0.001***
Year (2010)	3.02	0.90	3.34	<0.001***
Vegetation height × Year (2010)	-2.89	1.07	-2.69	0.008**
Vegetation height × Solar radiation	-0.53	0.46	-1.14	0.25

We used the data from the second session of 2010 to illustrate graphically exposure time above a given threshold temperature (from 30°C to 55°C) for any given vegetation height in the range 35-105 cm (Fig. 2b). As expected, exposure time decreases with vegetation heights but does so more rapidly as the temperature threshold increases (Fig. 2b). At 41°C (i.e. the lethal egg temperature), exposure time was low except for very low vegetation height (below 60 cm).

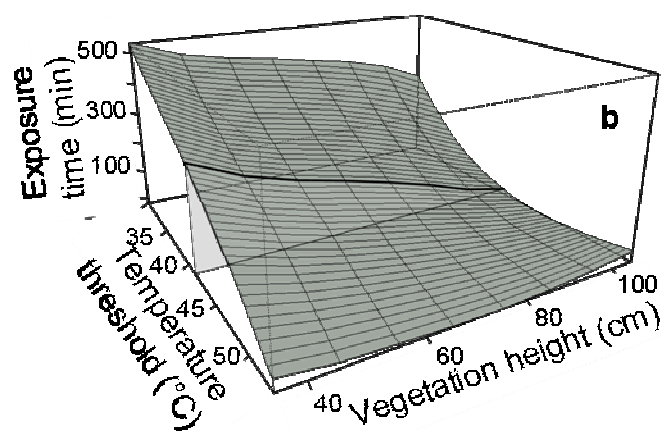
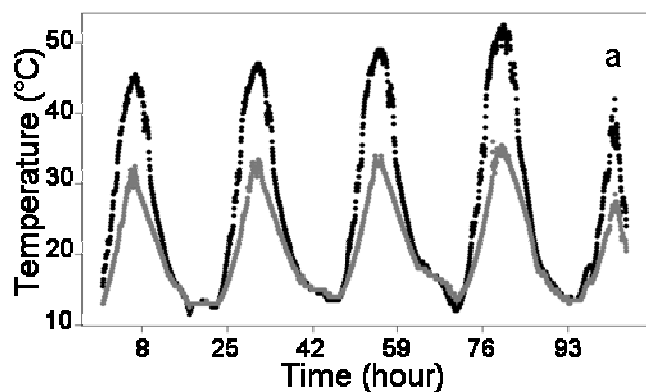


Figure 2: Temperature raw data of the intermediate session in 2010 (May 21-25<sup>th</sup>). (a) recorded temperatures of 2 loggers placed in low vegetation (30-40 cm, black dots ●) and in tall vegetation (100-110 cm, grey dots ●); (b) Daily exposure time (cumulative number of records) as a function of different threshold temperatures (30-55°C) and vegetation height. For information, the grey vertical plan in (b) represents the critical temperature (41°C) of most real eggs.

### Contrasting predation and overheating risks across spring

Using model predictions obtained from the two experiments, we explored graphically predation and overheating model outputs (GLMs and GLMM) according to vegetation height, egg color and season, as a way to build a conceptual representation of the relative importance of predation and overheating pressures over a breeding season (Fig. 3). 2010 was used to model both risks. Under temperate latitudes, figure 3 suggests that early in the breeding season (i.e. at low solar radiation), predation risks for both white and mimetic eggs could be more important than overheating risk (Fig. 3a). With the advance of spring, overheating risk increases with solar radiation, and at some undetermined stage in the season, overheating may exceed predation risk (Fig. 3b & 3c). Late in the season therefore, only very tall vegetation may reduce overheating risk (Fig. 3c).

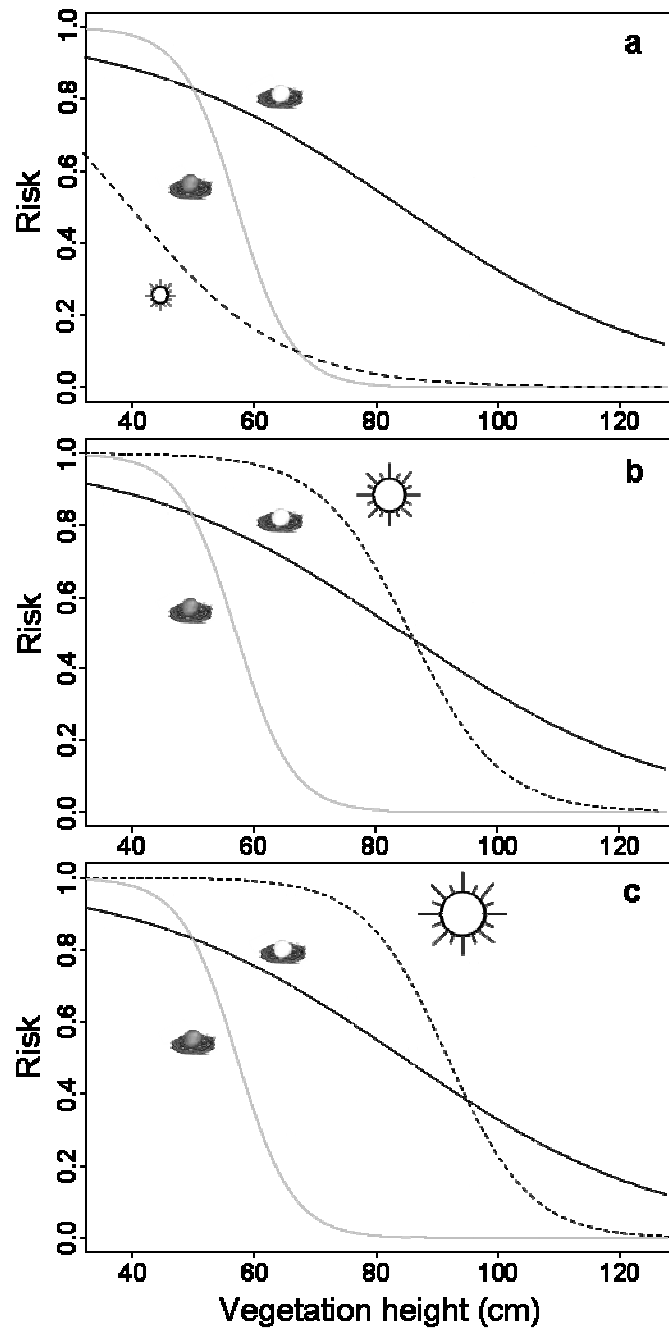


Figure 3: Conceptual representation of the relative importance of predation and overheating pressures over a breeding season using models' predictions for 2010. a), b) and c) respectively represent first, second and third sessions (gradient of solar radiation). Black and grey solid lines represent predation risk for white eggs and mimetic eggs respectively. Dashed lines represent overheating risk. The modelled predation rate for mimetic eggs was extrapolated to all the range of vegetation. "Risk" on the Y-axis represents predation rate or overheating risk predictions from the best fitted models.



## *Discussion*

In this study, we demonstrated that for ground-nests, predation and overheating risks decrease with vegetation height. We validated as well that egg coloration influences predation rate. Predation risk is constant over a breeding season while overheating risk presents inter- and intra-seasonal variations. As a consequence, we highlighted that the relative importance of the two selective pressures is unbalanced over a breeding season at least in temperate environment.

### Possible experimental bias

The use of artificial nests and dummy eggs to measure predation rates has long been disputed (Major and Kendal 1996, Moore and Robinson 2004), because of both positive (adults could defend nests, Davison and Bollinger 2000) and negative biases (adults could unveil nest location through their activity (Zuria et al. 2007, Moore and Robinson 2004)). Other biases have been identified, e.g. differences in local predator species preying upon artificial vs. natural nests (Martin 1987, Mezquida and Marone 2003), differences in nest and egg realism, egg type (plaster, plasticine, real quail eggs), and egg size (Bayne et al. 1997, Davison and Bollinger 2000, Dion et al. 2000). There is no consensus on how to conduct this type of experiment. However, as our aim was not to mimic real predation rates but only to detect the influence of nest characteristics (i.e. in absence of parents, Gregoire et al. 2003), we chose to use artificial nests and eggs to measure predation rates relative to nest concealment levels regardless of adult behavior (see also Howey et al. 1984, Davison and Bollinger 2000, Dion et al. 2000).

Similarly, temperatures measured by nest loggers do not correspond to core egg temperatures (Webb 1987). Real temperature experienced by the embryo may differ because heat transfer characteristics of egg is not taken into account in our experiment nor are egg coloration and adult incubation behavior. However, nest microclimate measured here must influence egg temperature. We modeled overheating risk using a temperature threshold of 41°C (15 minutes duration), as this temperature is usually lethal for bird embryos (Webb 1987). However, using different temperature thresholds lead to similar results (Fig. 2b): exposure time decreased monotonically with increasing temperature threshold and increasing vegetation height further reduced exposure time. Additionally, we did not measure differences in overheating between white and mimetic (green or dark) eggs. However, there is some





evidence that pigmented eggs get warmer than non-pigmented ones (Montevecchi 1976, Underwood and Sealy 2002, Magige et al. 2008; but see Westmoreland et al. 2007).

Obviously, as mentioned earlier, parental incubation behaviour (i.e. off- and on-bout durations and frequencies) play an important role in nest protection against both risks (Conway and Martin 2000). However, in this study we focused on the efficiency of concealment offered by vegetation to protect nest from predation and overheating regardless of parental behaviour. We believed that parental incubation behaviour could be influenced by the degree of nest concealment, a hypothesis already suggested by Conway and Martin (2000).

Therefore, we are confident that our experimental design provided a conceptual representation of the relative importance of predation and overheating pressures over a breeding season and along a vegetation height gradient for a ground nesting bird in a temperate environment.

#### Predation risk

Our study indicates that predation rate did not vary along a breeding season (no intra-seasonal variations) but did so between years. The former result is consistent with previous studies (Bayne et al. 1997, Burhans and Thompson III 1998), suggesting that the predator community does not change over a breeding season (Bayne et al. 1997). However, between-year variations suggest that some differences in predator community or behavior could have occurred between our two years of experimentation. Actually this year effect could result from differences in tested vegetation heights between years but also from three particular cases of mammalian predation in tall vegetation in 2010. However, the strong negative relationship between observed predation rate and vegetation height suggests that the predator community involved is mainly composed of avian predators because vegetation height should have less or no effect on nest detectability by mammals. These results are consistent with the predator marks on eggs. Moreover, our experimental results agree with previous studies that suggested that concealment is relevant where avian predators are dominant (Sugden and Beyersbergen 1986, Sugden and Beyersbergen 1987, Clark and Nudds 1991, Colwell 1992). In particular, Sugden and Beyersbergen (1987) studied predation on duck nests by American Crow *Corvus brachyrhynchos* according to concealment (vegetation density, height and type). They found a negative effect of vegetation height on predation rate. However, in their study



different vegetation heights were associated with different vegetation densities and types, a possible bias we avoided by using a single vegetation type and density.

We also found a significant difference in egg predation according to egg color. White eggs (i.e. the supposed ancestral egg color, Kilner 2006) may be less costly to produce than pigmented ones (Moreno and Osorno 2003). However, most ground-nesters choose to pay the energetic cost of egg pigmentation (Kilner 2006) to reduce predation risk (especially by avian predators, Castilla et al. 2007). Our experiment further revealed an interaction between vegetation height and egg coloration (a result also found by Castilla et al. 2007). At low vegetation height (< 50 cm), predation risk is high for both colors suggesting that neither color nor height are sufficient to avoid nest predation. However, above 60 cm, predation rate of mimetic eggs falls under 0.5; this particular threshold is reached for white eggs at 85 cm. Hence, nest concealment appears to be more efficient to provide protection against predation for mimetic eggs than for white eggs. This matches previous studies that also showed a lower detectability of mimetic eggs by predators (Solis and De Lope 1995, Castilla et al. 2007, Avilés et al. 2006) especially by avian ones (Castilla et al. 2007). Our results validate that egg coloration is less efficient than nest concealment to protect unattended eggs from predators (Underwood and Sealy 2002, Kilner 2006), since at very low vegetation (low nest concealment), mimetic and white eggs have very high predation rates (close to 1).

### Overheating risk

Our results support the hypothesis that structural cover (in our case, vegetation height) could influence nest microclimate conditions, in particular reduces temperature by shading eggs, and therefore ultimately may affect breeding success (Lusk et al. 2003). When parent brooding behavior is interrupted, eggs are exposed to sunlight: in such situation, vegetation cover could help maintaining temperatures at nest lower than those on bare ground and thus may provide a more stable thermal environment for developing embryos (Lusk et al. 2003). As expected, we found that overheating risk increased with season (i.e. solar radiation) and decreased with vegetation height. However, in 2009, very few nest temperatures  $\geq 41^{\circ}\text{C}$  were recorded in any session, hence no effect of solar radiation or vegetation height could be statistically detected. This may be as a result of cool and wet spring (soil moisture might have reduced the nest temperature) but also because taller vegetation plots were sampled in 2009 than in 2010, where a drier and warmer spring led to lower vegetation. Thus, in contrast to predation risk, overheating risk exhibited both inter and intra-seasonal variations. In 2010, if



overheating risk was minimal early in the breeding season, keeping overheating risk low required very tall vegetation at the end of the season. On the other hand, in temperate environments (where this experiment was carried out), breeding very early in the season (i.e. when solar azimuth angle is low) appears to be a good strategy to avoid overheating.

The between-year variation in overheating risk suggests that overheating may highly depend on climate conditions and wheat growth. In dry and warm years, overheating risk may be high because of high temperatures but also because of short vegetation. In the global warming context (higher temperatures and unpredictable precipitations), the importance of overheating risk for vegetation height selection should therefore be enhanced.

### Relative roles of predation and overheating risks

We believe our work shed light on behavioral and life-history traits evolution in ground-nesting birds. Overall, in any system, since predation risk may often be constant and overheating risk may change over a breeding season, the relative importance of these two risks are prone to change over a breeding season. These changes may have different consequences on birds' incubation effort (i.e. off-bout durations), nest defense (i.e. mobbing or lure-predator) and nest site selection behaviors according to their egg color and breeding timing. By laying mimetic eggs, detection by predators is reduced, but the risk of overheating could be enhanced (at least at temperate latitudes). The majority of ground-nesting birds lays mimetic eggs (Magige et al. 2008), and thus could face higher overheating risk (depending on egg shell pigments, see Bakken et al. 1978) than species that lay white eggs. Our study underlines two possible strategies to counteract this risk: conceal nest in tall vegetation, or breed as early as possible in the season to avoid high solar radiation. Most ground-nesting birds actually conceal their nests in dense and/or high vegetation cover (Colwell 1992). A third and complementary strategy, unexplored here, could be maintaining constant presence at nest or reducing off-bout durations. While birds laying white eggs are mainly cavity nesters (Blanco and Bertellotti 2002), which can be regarded as an extreme case of nest concealment, a few cryptic species also lay white eggs. These species could protect their eggs from predators by maintaining constant presence at nest (which necessitates bi-parental brooding) or reducing off-bout durations and/or frequencies or by concealing eggs in tall vegetation (the situation we explored in this study). Actually, ground-nesting birds laying white eggs could also protect their eggs against predators by defending the brood. This probably explains why Ostrich *Struthio camelus* lay white eggs on bare ground (Magige et al. 2008).



Montagu's harrier, by laying white eggs, does not pay the energetic cost for producing colored eggs. The present study however suggests that laying white eggs implies to select tall vegetation for nesting. This may represent a strong constraint early in breeding season, when females must establish their nests in crops that are around 80 cm high (to limit the main predation risk). Consequently, this pronounced habitat selection reduces suitable habitat availability. Later in season, they must select habitats at least 95 cm height (to limit both risks but especially overheating) but since wheat has grown, they may seem less selective according to vegetation height. This selection pattern according to vegetation height is actually observed in this species (unpublished data). Interestingly, this species does not perform bi-parental brooding to protect their eggs from predators: only female attends the nest and male brings her food which she eats most of the time out of the nest. However, this species further reduces this risk by its ability to defend the brood against predators, even using social defence since the species is colonial (see Arroyo et al. 2001 for an experimental demonstration of colonial defence). Apart from counteracting overheating risk, white eggs have another advantage: parents may benefit from locating the nest more easily and thus be able to nest in such a uniform farmland landscape (wheat crop; see Underwood and Sealy 2002, Avilés et al. 2006).

### **Acknowledgements**

We thank Martine Guérif, Jean Louis Martin and Alexandre Millon for helpful suggestions. Many people helped with egg confection and fieldwork, especially Vincent Lecoustre, Ramzi Guirat and Etienne Baron, and are kindly thanked. We also thank Janos Hennicke for valuable comments on the manuscript and for improving the English. ANR BIODIVAGRIM and ANR-ERANET ECOCYLCES partly funded this study. HG also wishes to thank the ED "Diversité du Vivant" for funding her PHD.



## **B.II. VARIATION TEMPORELLE DES PATRONS DE SELECTION DU SITE DE NIDIFICATION DU BUSARD CENDRE : INFLUENCE DES COMPOSANTES DE L'HABITAT**

### ***B.II.1. Résumé du chapitre***

Dans le chapitre précédent, nous avons comparé expérimentalement les pressions sélectives s'exerçant sur le choix d'une hauteur de végétation au nid par les oiseaux nichant au sol. Nous nous sommes intéressés pour cela à l'évolution saisonnière des importances relatives de ces pressions en zone tempérée. Dans cette partie, nous souhaitons :

(i) valider le schéma conceptuel mis en évidence dans le chapitre précédent en dégageant les patrons de sélection de hauteur de blé au nid du Busard cendré ;

(ii) évaluer l'effet des variations des composantes physique, biologique et sociale de l'habitat sur ce patron de sélection ;

(iii) examiner les conséquences de ce patron de sélection en terme de succès reproducteur ;

(iv) explorer et discuter les tendances à long terme observées dans le contexte du changement global.

Les méthodes et les résultats sont présentés et discutés en détail dans la partie en anglais de ce chapitre. Nous nous attachons donc ici à résumer succinctement les méthodes et les résultats tout en apportant des informations complémentaires pour expliquer les difficultés rencontrées et faciliter la compréhension globale.

Afin de mener à bien ce travail, nous disposons de bases de données à long terme sur notre zone d'étude : 18 ans de suivi exhaustif de la reproduction du Busard cendré et de suivi d'abondance de sa proie favorite, le campagnol des champs, et 16 ans de mesures de hauteurs de blé, milieu de nidification privilégié du Busard cendré.

Nous disposons des hauteurs de blé au nid à la date de première visite (variant suivant la date de découverte du nid). Il a d'abord fallu recalculer la hauteur au nid à une date permettant de comparer les hauteurs entre les nids. Nous nous sommes pour cela placés à la date de ponte (voir section en anglais pour son estimation) plutôt qu'à la date d'installation des individus, cette dernière n'étant pas connue. Afin de procéder aux estimations des



hauteurs de blé à la date de ponte de chaque nid, nous avons modélisé la croissance du blé à l'aide d'un modèle mécaniste utilisé en agronomie que nous avons appliqué aux données de hauteurs de chaque année (figure B.2).

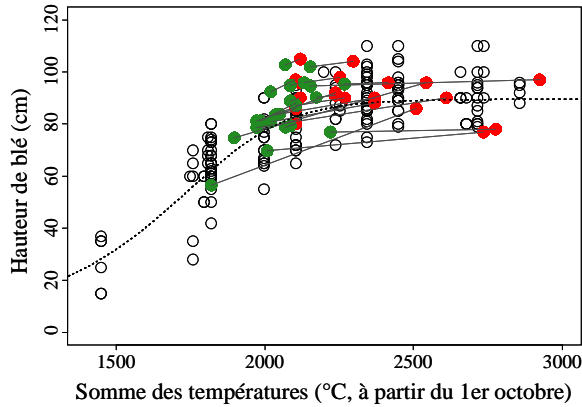


Figure B.2 : Représentation graphique des estimations de hauteurs aux nids à la date de ponte pour l'année 2001. La courbe pointillée représente la croissance moyenne du blé estimée par le modèle grâce aux hauteurs de blé mesurées (○). Afin de faciliter la lecture, des segments relient les hauteurs mesurées aux nids aux dates de visites (●) aux hauteurs aux nids estimées aux dates de pontes (●) grâce au modèle.

Une seconde difficulté résidait dans la grande disparité intra- et inter-annuelles des données de hauteurs de blé et dans la définition des hauteurs de blé disponibles pour chaque nid. En effet, les dates de ponte s'étaient tout au long de la saison de reproduction et chaque couple fait donc face à une disponibilité de hauteurs de blé différente (due à la croissance du blé). N'ayant pas à notre disposition plusieurs mesures de hauteurs disponibles à chaque date de ponte, nous avons choisi de travailler en hauteurs relatives par rapport à la valeur estimée par les modèles de croissance annuelles (résidus du modèle ; figure B.3). Une valeur positive de hauteur relative au nid indique que le couple s'installe dans une végétation plus haute que la hauteur moyenne disponible. Plus cette valeur est élevée, plus le couple s'installe dans des hauteurs importantes.

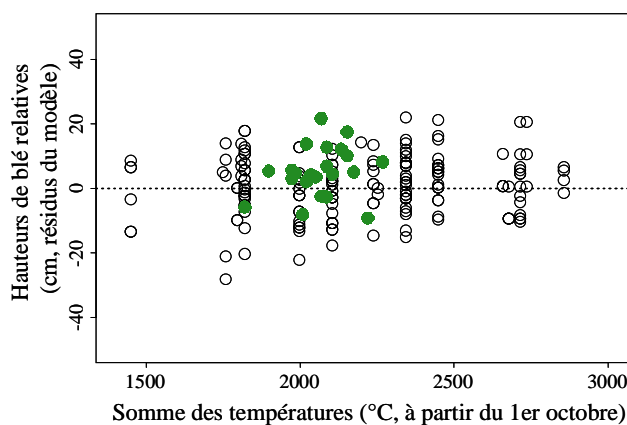


Figure B.3 : Représentation graphique des hauteurs relatives (●) aux nids à la date de ponte en 2001. La courbe pointillée représente la croissance moyenne du blé estimée par le modèle grâce aux hauteurs relatives de blé mesurées (○).



Nous avons ensuite examiné les patrons de sélection (hauteur relative au nid à la date de ponte) et l'influence de la phénologie annuelle du blé (composante physique), de l'abondance de campagnols (composante biologique), de la densité de nids (composante sociale) et de la date de ponte (afin de vérifier notre schéma conceptuel) sur ces patrons.

Afin d'explorer les effets des trois composantes de l'habitat sur la fitness, il nous fallait choisir au préalable le paramètre de la reproduction à considérer. Le succès de reproduction étant fortement biaisé par les protections (grillages) installées au stade poussin autour des nids afin d'éviter la destruction par les moissons puis la prédation par les mammifères, nous avons choisi d'utiliser le succès à l'éclosion et le taux de prédation au stade œuf comme paramètres de la fitness. Le succès à l'éclosion prend en compte toutes les causes d'échecs possibles dont celles liées à la hauteur du couvert : insolation et prédation des œufs. Cependant, certains échecs avant l'éclosion pouvant être liés à des causes anthropiques comme la destruction ou l'abandon du nid par la femelle suite aux travaux agricoles, nous avons également examiné le taux de prédation au stade œuf.

Enfin nous avons exploré les tendances à long terme des hauteurs disponibles, des hauteurs absolues choisies, de la sélectivité et des paramètres de la reproduction.

Les résultats obtenus pour la sélection de hauteur au nid d'une part et les paramètres de la reproduction d'autre part sont résumés dans le tableau B.1. Les busards sélectionnent globalement des hauteurs de blé plus importantes que la moyenne des hauteurs disponibles. La hauteur moyenne choisie est de 78 cm ( $\pm 12$ , N = 552 nids ; figure B.4). Ceci leur permet de limiter le risque de prédation au stade œuf. Les trois composantes de l'habitat influencent cependant à des degrés divers les patrons de sélection de hauteur de végétation au nid et les paramètres de la reproduction chez le Busard cendré (voir détails dans l'article).

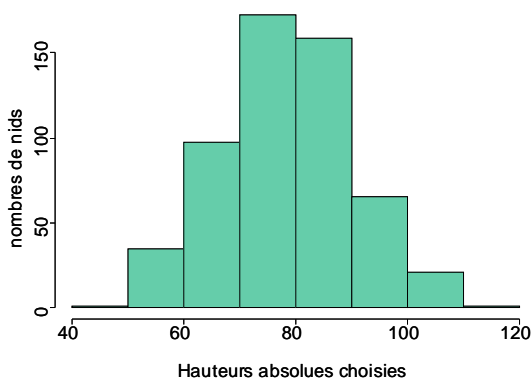


Figure B.4 : Distribution des hauteurs de blé (en cm) au nid au moment de la ponte (1996-2011, N = 552)

Tableau B.1 : Récapitulatif des résultats des modèles mixtes investiguant la sélectivité, le succès à l'éclosion et le taux de prédation au stade œuf.

Composante (variable explicative)	Sélectivité (hauteur relative au nid)	Succès à l'éclosion	Taux de prédation (stade œuf)
Biologique <sup>1</sup>	(+ +) *	.	.
Physique <sup>2</sup>	(- - -) *	(+) <sup>NS</sup>	(-) ***
Sociale <sup>3</sup>	.	.	(+) <sup>NS</sup>
Intra-annuelle <sup>4</sup>	(-) ***	(-) *	(+) **
Biologique × physique	.	.	.
Biologique × sociale	.	.	.
Biologique × intra-annuelle	(-) *	.	.

<sup>1</sup> Abondance de campagnols au printemps ; <sup>2</sup> Indice de phénologie du blé pour la sélectivité et hauteur de blé au nid pour le succès à l'éclosion et le taux de prédation au stade œuf ; <sup>3</sup> Nombre de voisins ayant déjà pondu pour la sélectivité, et nombre total pour le succès à l'éclosion et le taux de prédation au stade œuf ; <sup>4</sup> Date de ponte pour la sélectivité, et date de ponte relative (qualité du couple) pour le succès à l'éclosion et le taux de prédation au stade œuf.

Les symboles - ou + représentent le signe du coefficient estimé, et leurs nombres (de 1 à 3), l'importance relative des valeurs des coefficients estimés. Le niveau de significativité est indiqué à l'aide d'astérisques (<sup>NS</sup> : 0.1 < p, . : 0.05 < p ≤ 0.1, \* : 0.01 < p ≤ 0.05, \*\* : 0.001 < p ≤ 0.01, \*\*\* : p ≤ 0.001).

La sélection présente de fortes variations intra- et inter-annuelles en lien avec les trois composantes de l'habitat. Le lieu et le moment choisis pour se reproduire affectent également l'issue de la reproduction. Notre étude souligne donc l'importance de considérer les trois composantes de l'habitat afin de comprendre le choix d'un site de nidification et son impact sur les performances reproductrices. Ce travail confirme également qu'il est nécessaire de considérer l'hétérogénéité temporelle en utilisant des données à long-terme afin de comprendre l'influence de processus fluctuants et complexes mais aussi pour éviter toute interprétation erronée issue d'études à court terme.

Nous avons mis en évidence des tendances à long terme intéressantes suggérant que les effets du changement global (combinaison du changement climatique et de l'utilisation des sols) pourraient déjà être visibles sur notre zone d'étude sur une période de 16 ans : Les hauteurs moyennes de blé et l'abondance de campagnols diminuent poussant les busards à nicher dans une végétation plus basse. Ce phénomène est certainement amplifié par le caractère colonial de l'espèce (un couple s'installant dans une hauteur basse est susceptible d'en attirer d'autres). Par conséquent le succès à l'éclosion diminue en raison de l'augmentation du taux de prédation au stade œuf.





## ***B.II.2. Article 2***

### **Where and when to breed do matter: temporal variation in habitat features affect nest site selection and breeding performance in a ground-nesting raptor**

**H. GILLIS<sup>1\*</sup>, A. MILLON<sup>2</sup> and V. BRETAGNOLLE<sup>1</sup>**

<sup>1</sup> CNRS-UPR 1934, Centre d'Etudes Biologiques de Chizé, 79360, Beauvoir sur Niort, France

<sup>2</sup> CNRS-UMR 6116, Institut Méditerranéen de Biodiversité et d'Ecologie, Université Paul Cézanne, Europôle Méditerranéen de l'Arbois, avenue Philibert, BP 80, 13545 Aix-en-Provence cedex 04, France

\* Corresponding author: Hanneke Gillis

E mail: [gillis@cebc.cnrs.fr](mailto:gillis@cebc.cnrs.fr); [hanneke.gillis@yahoo.fr](mailto:hanneke.gillis@yahoo.fr)

Soumis à : **Oikos**



### *Summary*

Organisms select their breeding sites based on environmental cues that gather physical, biological and social components of habitat so as to maximise their fitness. When choosing a nest site, birds have to account for the two main selective pressures: predation risk and microclimatic conditions at nest. For ground-nesting birds, the physical characteristic of habitat (i.e. vegetation structure) has been identified as the most important factor determining nest site selection and in turn nest success. Using data collected over 16 years on a ground-nesting raptor nesting in wheat crops within an intensive farmland, we investigated the pattern of selection of vegetation height at the nest in a seasonally variable environment. We found that among years, Montagu's harriers select taller vegetation at their nest than available in average when wheat growth were delayed but also when prey abundance was higher, suggesting higher investment in reproduction in years where offspring prospects were good. However, they tend to be less selective on vegetation height when breeding in large colonies. Within a year, early breeders faced shorter wheat height and consequently were more selective towards taller cereal than available in average. In terms of breeding success, we found that isolated nests built in taller wheat by high quality pairs are less prone to predation at egg stage. Our study underlines the importance of accounting for all habitat features (i.e. physical, biological and social) in order to understand breeding habitat selection. Finally, temporal trends revealed a decrease in available and chosen wheat heights associated to an increase in egg predation rate. If current trends persist, long-term persistence of the breeding harrier population is thus questioned in such farming habitat.



## ***Introduction***

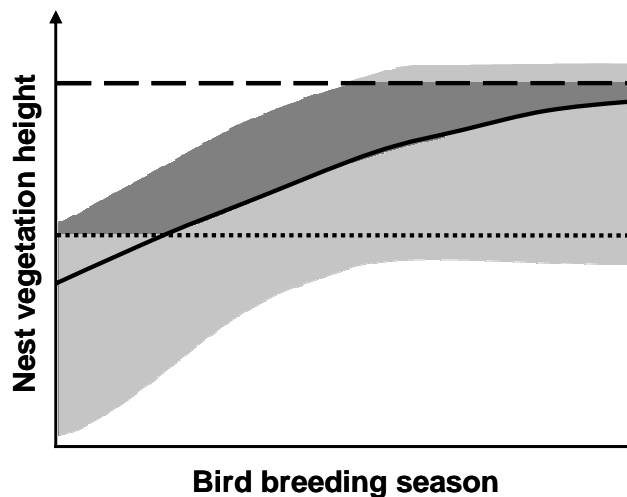
Animals select their breeding habitat based on a variety of environmental features that encompass i) physical features defining the abiotic characteristics of the habitat (e.g., altitude, temperature, humidity) and its vegetation structure (Bollinger 1995, Lusk et al. 2003, Kerns et al. 2010); ii) biological features including food resources but also abundance of natural enemies (predators and parasites; Davis 2005); and iii) social features, or the presence of conspecifics or heterospecifics potentially in interaction (competition Bollinger(1995) or facilitation; Hurd 1996, Hahn and Silverman 2006). Breeding habitat selection is expected to rely on these three habitat components (i.e., physical, biological and social) so as to maximise fitness (Danchin et al. 1998, Jones 2001).

In oviparous species like birds, selection of breeding habitat is particularly important to ensure embryo development and protection as eggs develop externally (Hansell and Deeming 2002). Bird nest sites are generally fixed locations where eggs and chicks can survive, at least short time periods, in the absence of parents (Hansell and Deeming 2002). Vegetation structure (e.g. height, density, bare ground percentage, species composition) is regarded as the most important feature determining nest site selection (Bollinger 1995), particularly for ground-nesting species which usually face higher direct lethal costs of ill selection compared to cliff-, tree- or cavity-nesters (Limiñana et al. 2006). Indeed, nests built on the ground generally suffer high risks of predation, the main source of nest failure in birds (Ricklefs and Institution 1969), as well as overheating (Deeming 2002, Walsberg 1985, Lusk et al. 2003, Wilson et al. 2005). Grassland birds in particular have received much attention, and most studies pointed out the key role of vegetation structure (Bollinger 1995, Helzer and Jelinski 1999). Grassland and steppe birds have adopted a wide set of behavioural strategies that range between two extremes. Some species nest in low and sparse vegetation and so doing, favour visibility around the nest to detect predators. Such species have highly mimetic eggs and chicks (adults are usually inconspicuous too), and maintain constant presence at nest, like waders (e.g., Stone-curlew *Burhinus oedicanus*, Wilson et al. 2005). At the other extreme, some species promote nest concealment by nesting in tall and dense vegetation to protect their nest against predators and extreme weather conditions (e.g. sage grouse *Centrocercus urophasianus*, DeLong et al. 1995).

Ground-nesters may achieve nest concealment by selecting tall vegetation so as to reduce nest predation and egg overheating (Gillis et al. [a]. in review, Fig. 1). Alternatively,



they may select intermediate or low vegetation allowing adults to safely escape nest in case of a predator attack (Low et al. 2010) and to avoid feather abrasion (Cresswell 1997), indicating that nest accessibility constraints also exist (Fig. 1). In addition, ground-nesting birds are further constrained by vegetation height availability, which varies seasonally, at least under temperate latitudes where vegetation grows over the breeding season and overheating constraint increases with solar azimuth (Fig. 1). According to vegetation growth and the relative importance of the three constraints (i.e. nest predation, overheating and accessibility), we expect individuals to be highly selective toward relatively taller vegetation early in the season, but less selective later in the season (Fig. 1).



*Figure 1: Schematic representation of the constraints involved in selection for vegetation height at the nest in a ground nesting bird over a breeding season where vegetation is growing. The dotted and solid lines respectively represent the required height to avoid nest predation and to avoid direct solar exposition thus egg or chick overheating. The dashed line represents the height threshold above which accessibility and probability of escaping predators for adults are reduced. The grey area represents the suitable (dark grey) and unsuitable (light grey) vegetation heights among those available. According to constraints and date in the season, the dark grey area represents the vegetation heights ground nesting bird should select for. All the system (constraints and available heights) or only some component(s) of the system could change according to annual vegetation phenology, food abundance and presence of conspecifics. For instance, early vegetation phenology could offer taller vegetation in early season. High prey abundance should lead individuals to be more selective. Finally, conspecific presence could alter any selection pattern if conspecific attraction occurs.*

Additionally, among-year variation in vegetation phenology or food resource abundance may alter the pattern of selection. For instance, fluctuations in food abundance affect predator breeding investment (Whittingham and Robertson 1994, Korpimäki 1992): when food abundance is high, individuals generally lay larger clutches (Millon et al. 2008). Since larger clutches are more detectable by predators (Martin 1995, Eggers et al. 2006, Travers et al. 2010), individuals should breed in taller vegetation to minimize nest predation

probability. Finally, the third component of habitat selection, i.e. the presence of conspecifics, may also affect nest site selection, leading to skewed nest distribution (Danchin and Wagner 1997) in comparison to expected distribution based on real vegetation structure quality. If intra-specific attraction occurs because of group defence reducing predation risk (Doligez et al. 2003), then birds will aggregate and be less selective on vegetation structure.

To date, very few studies have simultaneously investigated the relative influences of physical, biological and social features of habitat on small-scale nest-site selection. Here we used a ground-nesting raptor, the Montagu's harrier *Circus pygargus*, as a case study, to infer on the processes leading to nest-site selection. In Western Europe, this species breeds in intensively managed agricultural crops (mainly winter cereals). Several studies already revealed the importance of vegetation height in determining nest location in this species (Claro 2000, Arroyo et al. 2004, Limiñana et al. 2006). Our study population breeds mostly in a single crop type (80 % of nests in wheat) in a farmland landscape. Wheat height is highly variable among fields, years and season. Montagu's harrier is further specialised on the Common vole *Microtus arvalis*, which is a cyclic prey in our study area, with strong among-year variations in abundance (Lambin et al. 2006). Finally Montagu's harrier is a facultative colonial breeder, with solitary pairs as well as colonial pairs simultaneously. Since vegetation height, food abundance and local density are highly variable within and between years, and are uncorrelated to each other, we were able to investigate their effects (including their interactive effects) on a proxy of micro-habitat choice, i.e. vegetation height. We then quantified the consequences of selected vegetation height at nest as well as vole abundance, pair quality and number of neighbours on two fitness components: hatching success and egg predation rate). Finally, since our study covered 16 years we explored potential long-term trends in vegetation height selection and fitness components.

More specifically, we predicted that harriers select fields with tall vegetation for nesting to reduce predation and overheating risks. Further, we predicted that the strength of selection for tall nest vegetation should decrease with i) season (because of wheat growth and/or accessibility constraint), ii) wheat growth precocity, and iii) number of neighbours in the colony, while it should iv) increase with vole abundance.



## ***Materials and methods***

### Study area

This study was carried out in an intensively managed farming landscape located in central-western France (Deux-Sèvres: 46°11'N, 0°28'W). The study area covers nearly 500 km<sup>2</sup>, and crops are dominated by cereals (>40% of total surface), colza and spring-sown crops (mainly maize and sunflower). Though cereal crops are characterised by highly homogeneous within field vegetation structure (height, density and species composition), at a landscape scale however, there is a wide between-field variability in vegetation height, due to differences in agricultural practices in addition to soil characteristics.

Since 1994 and every year, land use has been monitored for each of the ca. 19,000 fields of the study site. From 1996 to 2011, we measured wheat heights over the entire study area and at different times during crop growth (from April 1<sup>st</sup> to June 30<sup>th</sup>). A total of 4550 measurements to the nearest 5-centimetres were performed on 1438 different fields using a rigid ruler. Each wheat field was measured from 1 to 11 times (mean = 3.2 measurements) in a single location at 15 m meters from the edge. Only one measurement per field was performed, since agricultural practices result in extreme homogeneity in vegetation structure within a field.

### Study species

The Montagu's harrier *Circus pygargus* is a trans-saharan migratory raptor, breeding in Europe and Central Asia. In Western Europe, nests are found in farmland (mainly in winter cereals; Cramp and Simmons 1980, Arroyo et al. 2002, Arroyo et al. 2004). Nowadays, cereal crops seem to be the most frequent breeding habitat of this species in France (>70 % of nests; Arroyo et al. 2002). While some breed solitarily, most pairs breed in loose colonies gathering 2 to 30 pairs ( Arroyo et al. 2002, Arroyo et al. 2004). In French farmland particularly, breeding density and breeding success of this predator are strongly affected by the abundance of its main prey, the common vole *Microtus arvalis*, a microtine rodent which constitutes 60–90% of its diet in biomass (Butet and Leroux 1993, Arroyo 1998; Salamolard et al. 2000; Millon et al. 2002). To account for the effect of its main prey on breeding parameters, an index of vole abundance in spring (April of each year) was estimated annually using line-trapping (see Salamolard et al. 2000 for more details).



From 1996 to 2011, all nests were located ( $N = 887$ , 14–104 nests/year) through an intensive searching effort (see Millon and Bretagnolle 2008 for details). Among these, 701 nests (79 %) were located in wheat fields. Therefore, and to avoid confounding effects of vegetation density and type, we focused our analysis on nests located in wheat only. Nests were visited as early as possible and vegetation height at the nest was measured at the first visit using a rigid ruler to the nearest centimetre. Nests were then regularly checked to collect data on laying date, clutch size, hatching and fledging success and predation events. Laying date was directly estimated for some nests visited during laying or back-calculated from chick and/or egg measurements (see Millon et al. 2002). As much as possible, causes of nest failure before hatching were identified by signs left at the nest. Predation events were clearly identified as shell fragments were found on the nest. No partial clutch predation was ever recorded during our study. Nests destroyed by harvesting activities at egg stage were excluded from the analysis of the effect of nest vegetation height on egg predation. Breeding parameters and nest vegetation heights in wheat fields were available for 552 nests. Additionally, we recorded the number of neighbours installed in the surroundings of each nest (i.e. within a 750m radius see Cornulier and Bretagnolle 2006 for radius choice explanation) to assess the effect of conspecific presence (i.e. social habitat feature).

#### Estimating wheat height at the date of laying

Nest could be discovered (and therefore visited) at any time of the season although most nests were found early in the breeding phenology (> 75% before hatching). Vegetation height at the date of laying was thus estimated using a mechanistic model (Debouche 1979):

$$H = \frac{H \max}{(1 + \exp(-Vpi \times (ST - Spi)))^n} \quad \text{Eqn. 1}$$

with  $H$ , the height at a given time;  $Hmax$ , the maximum height reached;  $Vpi$ , growth rate at inflexion point;  $ST$ , the sum of temperature (since 1<sup>st</sup> October the previous year);  $Spi$ , the inflexion point and  $n$ , a shape parameter. We used the sum of temperature instead of day because wheat development is closely linked to temperature (which differs between same days of different years) and to photoperiod (which, for a given latitude, is equal for the same day of different years; Geslin 1944). Wheat growth model parameters were established using all wheat fields except the ones occupied by harriers to ensure data independence when calculating vegetation height availability. As we expected inter-annual variation in wheat growth and maximum height reached, we ran models for each year separately. Annual model



parameters were estimated by the least-squares method. For five years (2000, 2003, 2005, 2006 and 2007), model did not converge, presumably because of insufficient data. Fixing  $V_{pi}$ , the least variable parameter across the ten other years (extremes: 0.005-0.025, coefficient of variation = 0.47) to its mean value (0.011), allowed the model to converge. Year-specific growth models were then used to recalculate  $H_{max}$ , given first visit date (expressed as sum of temperature for replacement of  $ST$  in Eqn. 1) and wheat height at first visit. We subsequently estimated wheat height at the date of laying. Finally, we obtained relative wheat height at the nest at laying date by subtracting estimated wheat heights from modelled ones. This final step allows us to compare the patterns of wheat height selection by harriers, both within and among years.

Additionally, an index of wheat phenology was calculated for each year from the growth model, as the date at which wheat reached 70 cm (corresponding to the first quartile of wheat height at the nest).

### Statistical analysis

We first performed an analysis of variance to check for the existence of within- and among-year variations in absolute and relative nest wheat height, hatching success and egg predation rate. Laying date and its quadratic term (continuous) were used as explanatory variables addressing within-year variation, while year (a 16 level-factor) was used for addressing among-year variations. We then used Generalized Linear Mixed Models (GLMM) to investigate the sources of variation in relative nest wheat height selection, in hatching success and in egg predation rate. Adequate error distributions were identified: Gaussian for wheat height, binomial for hatching success and egg predation. Years were treated as a random factor to account for all sources of heterogeneity associated with years besides variation in vegetation phenology and vole abundance (see appendix A1 and A2 respectively for year-to-year variation). Laying date, yearly wheat phenology index, vole abundance (log10-transformed) and neighbours already installed at laying date of target nest (since forthcoming pairs will not influence target nest location) were included in the model investigating variation in selection of relative wheat height at the nest. Vole abundance, absolute wheat height at the nest, relative laying date (as a proxy of the quality of the pair: (Salamolard et al. 2000, Arroyo et al. 2007) and total number of neighbours were included in model performed on hatching success and predation rate. Dates were expressed in Julian days with April 1st = 1. For each model, we tested all second order interactions involving spring





vole abundance because vole abundance is known to deeply influence many Montagu's harrier breeding parameters (Salamolard et al. 2000, Arroyo et al. 2004, Millon et al. 2002, Millon and Bretagnolle 2005, Millon et al. 2008). We checked for correlations (i.e. Spearman correlations between annual variables, Pearson correlations otherwise) between variables. If the correlation between two variables was strong (i.e.  $r > |0.5|$ ), one of the two variables was suppressed, keeping the variable explaining the most of the variance. We then standardized all continuous explanatory variables to facilitate comparison of effects through coefficients. Since *a priori* hypotheses were tested, we did not perform model selection. Only significant relationships are graphically represented by partial regression plots. We further explored potential long-term trends in available and chosen wheat heights, in hatching success and egg predation rate by using Spearman correlations on annual mean values.

Descriptive statistics are expressed as mean  $\pm$  standard deviation. Statistical procedures were performed using R (version 2.12.1, R Development Core Team, 2010). The "glmer" function ("lme4" package) was used to perform GLMMs.

### **Results**

At the date of laying, mean wheat height chosen by harriers for nesting was 78 cm ( $\pm$  12, N = 552 nests). This mean value however varied strongly among years from  $70 \pm 8$  in 2008 to  $89 \pm 11$  in 2000 ( $F_{15,536} = 16.8$ ,  $P < 0.001$ , Fig 2a). Additionally, wheat height at the nest increased initially then stabilised by the very end of the season (quadratic term:  $F_{1, 550} = 59.42$ ,  $P < 0.001$ , linear term:  $F_{1, 549} = 75.06$ ,  $P < 0.001$ ; Fig. 2b). On average, Montagu's Harriers selected wheat fields that were about 5 cm taller than available ones (as shown by intercept value in Tab. 1). Once more however, strong among-year variations occurred in the pattern of selection ( $F_{15, 536} = 17.9$ ,  $P < 0.001$ , Fig. 2c). Indeed, if harriers showed positive selection (i.e., for taller than average wheat fields) in most years (9 out of 16), no significant selection was detected for 6 years, and negative selection occurred in one year (Fig. 2c). Additionally, selection for taller than average wheat fields decreased with season (quadratic term:  $F_{1, 550} = 27.1$ ,  $P < 0.001$ , linear term:  $F_{1, 550} = 30.9$ ,  $P < 0.001$ ; Fig. 2d). In other words, harrier selected for taller than average wheat height early in the breeding season and showed no selection in the middle and late breeding season (even some cases of negative selection in late season). There was less than 20 cm in magnitude (25-75% quantiles = 70-87 cm, N = 552



necks) in wheat height at the nest between early and late breeders, while in the same time, wheat height increased by about 60 cm over the complete laying period.

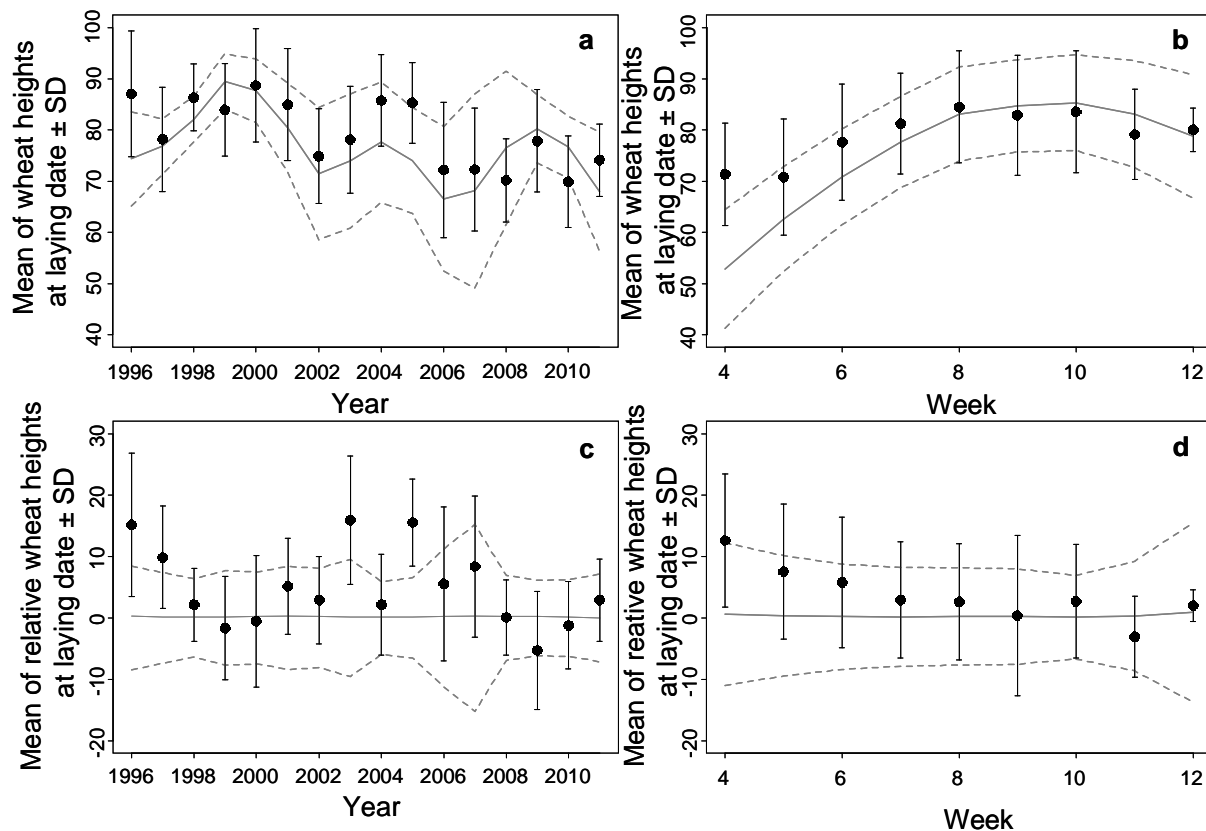


Figure 2: Among- and within-year variations of absolute (a & b) and relative wheat heights (c & d). Grey solid lines represent mean values of available wheat heights ( $\pm$  SD: dashed grey lines) while black dots represent mean values of chosen wheat heights ( $\pm$  SD: black error bars). Week-axis is expressed in “julian weeks” (1 = 1<sup>st</sup> week of April).

Wheat phenology index was positively related to the vole abundance index (Spearman correlation:  $r = -0.44$ ), suggesting that late years in terms of vegetation growth were also poor years in terms of vole abundance. Other correlation coefficients did not exceed 0.35. We found that harriers significantly selected taller wheat fields in years when wheat growth was delayed (i.e., negative values of wheat phenology index; see Tab. 1 and Fig. 4a). Additionally, when vole abundance was low, no selection or even selection for lower fields was observed, whereas when vole peaked in abundance, harriers strongly selected taller wheat fields (Tab. 1, Fig. 4b). Early breeders significantly selected for taller than average available wheat height, conversely to late breeders (Tab. 1, Fig. 4c), as they typically face shorter vegetation. Additionally, when vole peaked in abundance, the more a pair had neighbours the less it tended to select tall wheat among those available (Tab. 1, Fig. 4d).



Table 1: Generalized linear mixed model investigating relative wheat height at the nest in Montagu's harrier. Estimated coefficients (Estimate), standard errors (SE), t statistic and P-values are presented. Before running the model, all variables were standardized. Spring vole abundance was log-transformed and Wheat phenology index was multiplied by -1 afterward (to facilitate interpretation, i.e. low values = delayed phenology & high value = advanced phenology). Years were treated as a random factor. Number of neighbours was counted within a 750-m radius at the date of laying for each nest.

variable	Estimate	SE	t	P
<b>Intercept</b>	<b>5.48</b>	<b>1.53</b>	<b>3.56</b>	<b>&lt; 0.001</b>
<b>Spring vole abundance (log<sub>10</sub>)</b>	<b>4.44</b>	<b>1.77</b>	<b>2.27</b>	<b>0.03</b>
<b>Wheat phenology</b>	<b>-6.34</b>	<b>2.27</b>	<b>-2.79</b>	<b>0.01</b>
<b>Laying date</b>	<b>-1.74</b>	<b>0.43</b>	<b>-4.06</b>	<b>&lt;0.001</b>
Number of neighbours	-0.12	0.44	-0.27	0.78
Spring vole abundance × Wheat phenology	-0.75	1.33	-0.56	0.58
Spring vole abundance × Laying date	0.21	0.39	0.53	0.60
<b>Spring vole abundance × Number of neighbours</b>	<b>-0.81</b>	<b>0.42</b>	<b>-1.95</b>	<b>0.05</b>

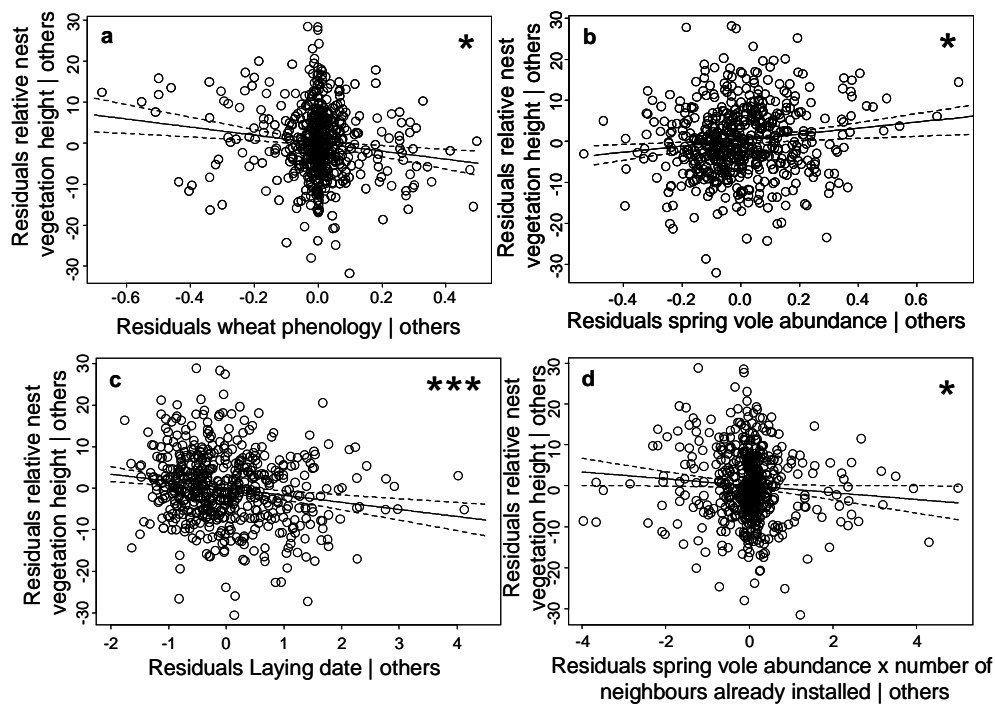


Figure 4: Partial regression plots of selection of relative wheat heights at the nest to significant dependent variables: (a) wheat phenology index, (b) log-transformed spring vole abundance, (c) laying date, and (d) the interaction between spring vole abundance and the number of neighbours already installed. All variables were standardized. Spring vole abundance was previously log-transformed and wheat phenology index was multiplied by -1 after standardization (to facilitate interpretation, i.e. low values = delayed phenology & high value = advanced phenology). For each plot: Y-axis represents the residuals of a GLMM performed with the independent variable and all dependent variables except the one on the X-axis; X-axis represents the residuals of a GLMM performed with the target variable against all other dependent variables. Dashed lines represent 95% confidence intervals.



Overall, 38.2% (N = 211) of the 552 monitored nests failed. From these 211 nests, 37.9% (N = 80) failed at egg stage, 55.9% (N = 118) at chick stage, 2.8% (N = 6) at hatching stage and 3.3% (N = 7) at an unknown stage. Hatching success did not significantly differ among years ( $\chi^2_{15} = 13.2$ , P = 0.59, Fig. 3a) and within year (Quadratic term:  $\chi^2_1 = 0.88$ , P = 0.38, linear term:  $\chi^2_1 = 0.38$ , P = 0.54).

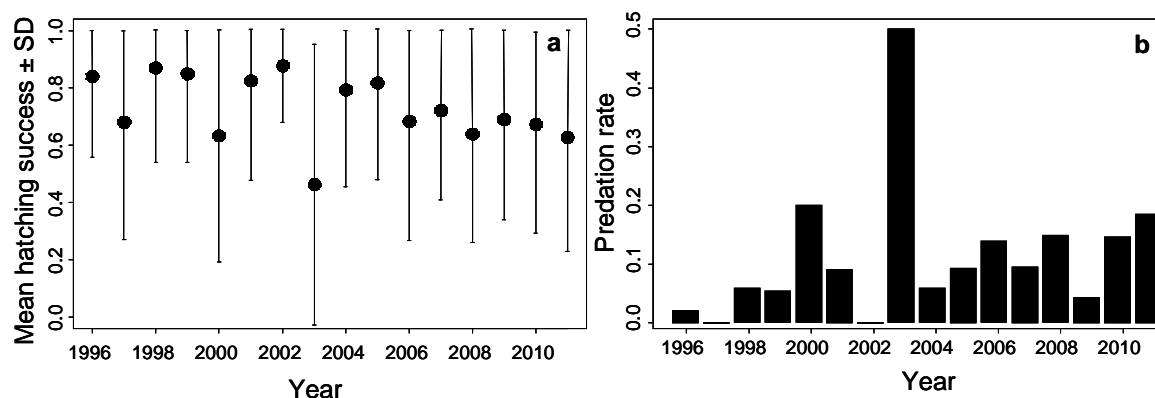


Figure 3: Annual variations in (a) mean hatching success (number of hatchling/clutch size)  $\pm$  standard deviations and in (b) egg predation rate (proportion of nests depredated at the egg stage).

Hatching success was found to decrease with relative laying date that is to say, to increase with pair quality. It also tended to increase with absolute height at the nest (Tab. 2a). From the 80 nests that failed at egg stage, 53 were predated (66%), the remaining failures being mostly induced by harvesting activities. Using only the 53 predated nests that failed at egg stage, as well as all nests that were successful at least until hatching, the total number of remaining nests for our predation rate modelling was 518 nests. We detected strong among-year variation in the proportion of nests predated at the egg stage ( $\chi^2_{15} = 35.9$ , P = 0.002, Fig. 3b), but no within-year variation (quadratic term:  $\chi^2_1 = 0.34$ , P = 0.56, linear term:  $\chi^2_1 = 0.49$ , P = 0.48). Predation rate significantly decreased with wheat height at the nest (Tab. 2b, Fig. 5a), suggesting that tall vegetation effectively protect eggs against predators. Additionally, predation rate also increased with relative laying date and thus decreased with pair quality (Tab. 2b, Fig. 5b), and tended to increase with the number of neighbours settled in the colony (Tab. 2b, Fig. 5c), revealing the more a nest had neighbours (regardless of their reproductive stage) the more it was prone to predation.



Table 2: Generalized linear mixed model investigating hatching success (a) and egg predation rate (b) in Montagu's harrier population. Estimated coefficients (Estimate), standard errors (SE), z statistic and P-values are presented. Years were treated as a random factor. Each variable was standardized and all neighbours were counted within a 750-m radius around each nest.

a) Hatching success

variable	Estimate	SE	z	P
<b>Intercept</b>	<b>-0.29</b>	<b>0.04</b>	<b>-7.98</b>	<b>&lt;0.001</b>
Spring vole abundance (log <sub>10</sub> )	0.04	0.04	1.06	0.29
<b>Absolute nest height at the date of laying</b>	<b>0.07</b>	<b>0.04</b>	<b>1.79</b>	<b>0.07</b>
<b>Relative laying date</b>	<b>-0.10</b>	<b>0.04</b>	<b>-2.53</b>	<b>0.01</b>
Number of Neighbours in 750-m radius	-0.04	0.04	-0.94	0.35
Spring vole abundance × absolute nest height	0.003	0.03	0.09	0.93
Spring vole abundance × Relative laying date	-0.002	0.04	-0.07	0.94
Spring vole abundance × Number of Neighbours in 750-m radius	0.02	0.03	0.76	0.44

b) egg predation rate

variable	Estimate	SE	z	P
<b>Intercept</b>	<b>-2.27</b>	<b>0.20</b>	<b>-11.03</b>	<b>&lt;0.001</b>
Spring vole abundance (log <sub>10</sub> )	-0.16	0.23	-0.68	0.49
<b>Absolute nest height at the date of laying</b>	<b>-0.63</b>	<b>0.19</b>	<b>-3.33</b>	<b>&lt;0.001</b>
<b>Relative laying date</b>	<b>0.40</b>	<b>0.16</b>	<b>2.59</b>	<b>0.009</b>
<b>Number of Neighbours in 750-m radius</b>	<b>0.30</b>	<b>0.16</b>	<b>1.81</b>	<b>0.07</b>
Spring vole abundance × absolute nest height	-0.32	0.22	-1.464	0.14
Spring vole abundance × Relative laying date	-0.04	0.16	0.28	0.78
Spring vole abundance × Number of Neighbours in 750-m radius	-0.23	0.17	-1.33	0.18

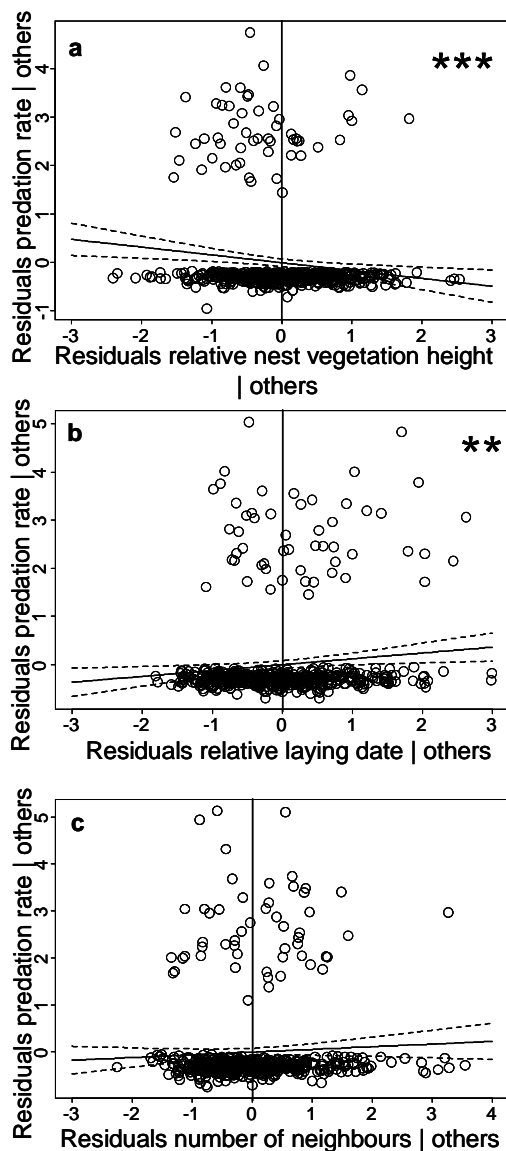


Figure 5: Partial regression plots of egg predation rate to significant dependent variables: (a) absolute nest wheat height, (b) relative laying date (i.e. pair quality) and (c) number of neighbours in 750 m radius. All variables were standardized. For each plot: Y-axis represents the residuals of a GLMM performed with the independent variable and all dependent variables except the one on the X-axis; X-axis represents the residuals of a GLMM performed with the target variable against all other dependent variables.

Interestingly over the course of our 16-year-study, mean available wheat heights tended to decrease ( $\rho = -0.42$ ,  $P = 0.1$ ), mean chosen absolute heights strongly decreased ( $\rho = -0.74$ ,  $P = 0.001$ ) while mean relative heights did not exhibit long-term changes ( $\rho = -0.25$ ,  $P = 0.34$ ). It suggests that even if wheat became lower, harriers did not adapt their selection by nesting in relatively taller wheat fields among those available as might be expected. They actually tended to select the reverse. Additionally, mean hatching success decreased ( $\rho = -0.49$ ,  $P = 0.05$ ) and egg predation rate increased ( $\rho = 0.5$ ,  $P = 0.05$ ).



## *Discussion*

Selection pattern for vegetation height at the nest indicated that Montagu's harriers selected relatively taller heights compared to availability. Selected heights remained within a relatively narrow window along the season (70-90 cm), despite strong changes in availability with season. Selection was therefore not static, since we detected marked within- and among-year variations in wheat height selection, part of the variation being directly linked to vegetation phenology, food availability and social context. Our study highlights the importance of accounting for the three habitat components (i.e. physical, biological and social features) to understand nest-site selection and its impact on the breeding performance (Bollinger 1995). Finally, while the choice of a particular vegetation height only slightly influenced hatching success, it strongly affected egg predation rate. Where and when to breed therefore affect the outcome of reproduction in this species.

### Temporal variations in nest-site selection

The selection of a particular wheat height at the nest by harriers appears to be mainly driven by physical (i.e. vegetation phenology) and biological (i.e. prey abundance) components. Wheat phenology strongly varies across years, certainly as a consequence of variations in agricultural practices, precipitations and temperature (Chamberlain et al. 2000). When wheat phenology is early, availability of tall wheat fields is increased, and more wheat fields reach the threshold value (i.e. about 80 cm) for nesting harriers. As a consequence, harriers appear less selective in those years. Additionally, harriers can be exposed to strong annual variation in food availability, and particularly in Western France where common vole populations show cyclic dynamics (Lambin et al. 2006). Our results demonstrate that when vole abundance is low, harriers are less selective with regard to wheat height. On the contrary when vole abundance is high, harriers nest in tall wheat and are highly selective in favour of taller wheat than available in average. This pattern was expected under the hypothesis of differential breeding investment according to vole abundance. Indeed, when vole abundance is high, offspring prospects are good leading harriers to lay larger clutches (Millon et al. 2008), which are potentially more detectable by predators (Martin 1995, Eggers et al. 2006, Travers et al. 2010). An other but not mutually exclusive hypothesis could result from differential spatial distribution of voles according to cycle phase: when vole abundance is low, vole distribution may be heterogeneous over the study area, constraining harriers to nest



in available wheat fields (not necessary tall) close to the prey resources. On the contrary, when vole abundance is high, voles may be uniformly distributed over the study area allowing harriers to be selective to the benefit of tall wheat fields. Under this scenario, habitat selection in harriers would be hierarchical and acting at multiple scales (Johnson 1980): the first harriers select an area according to vole abundance, and in a second time they select a field according to vegetation structure.

In addition to inter-annual variations, selection varied within a breeding season. Actually, the pattern of selection found in this study is consistent with differential roles of predation risk, overheating and nest accessibility as depicted in Figure 1. When harriers are late breeders, they find taller vegetation height and therefore can be less selective. Interestingly, in this species as in many others (Daan et al. 1988, Meijer et al. 1990), laying date correlates negatively with pair quality (Salamolard et al. 2000, Arroyo et al. 2007). Early breeders (i.e. high quality pairs) lay larger clutches (Arroyo et al. 2007), that may require higher levels of concealment (i.e. tall vegetation at nest) to counteract superior risk of detection by predators (Perrins and Moss 1975). In contrast, late breeders (i.e. poor quality pairs) lay less detectable small clutches, which require less concealment (Perrins and Moss 1975). Additionally, high-quality pairs should be able to better assess patch quality (i.e. field wheat height) than late poor-quality ones (Valone 2007). Finally, when vole peak in abundance, harriers having many neighbours were less selective on wheat height. This pattern suggests that attraction occurs and that birds breeding in colonies may rely on group defence rather than wheat height at the nest to reduce predation risk.

#### Fitness consequences of nest vegetation height choice

The choice of nest site often affects reproductive performance, although it does not always indicate optimal choice in terms of nest success (Clark and Shutler 1999). Indeed, we only detected a small effect (in terms of statistical magnitude) of nest site selection on hatching success. A much stronger effect was detected with regard to egg predation rate, perhaps because hatching success also depends to a large extent on anthropogenic factors in this species (e.g., crop harvesting). Our study confirmed that nest vegetation height could be efficient to protect harrier eggs against predators. Contrary to Arroyo et al. 2001 who found that nest predation was lower in colonies than in solitary pairs because of conspecific cooperation for mobbing predators, we found that increasing number of neighbours increased predation rate. This discrepancy certainly results from differences in the way nest predation





was measured, since Arroyo et al. 2001 measured total predation rate (i.e. both egg and chick stages). Additionally, cooperative defence is more efficient for predators like raptors or foxes than for crows, the main predator of eggs (Arroyo et al. 2001, Arroyo et al. 2004). Besides, high parental activity in colonies may unveil nest positions to crows (Martin et al. 2000).

#### Management implications of observed long-term trends

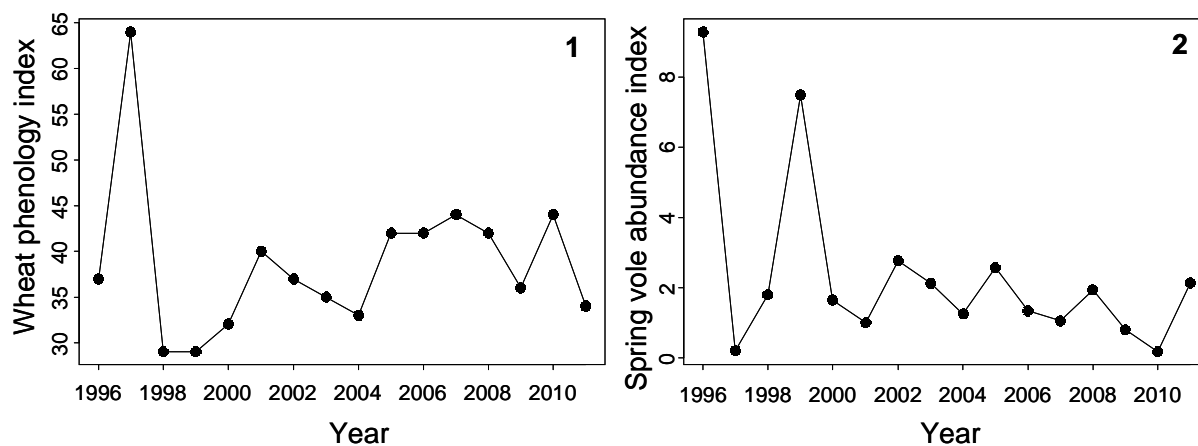
In certain areas of France and Spain, ca. 60% of harrier nests would be destroyed by harvesting activities in absence of direct protection measures. Such a level of destruction is not sustainable by the population without immigration (Arroyo et al. 2002). The Montagu's harrier is thus particularly dependent on changes occurring in its habitat, due to agricultural practices and climate change. Improving our knowledge about nest site selection is therefore of paramount importance for the conservation of Montagu's harrier in intensive farming areas. Both agricultural practices (e.g. use of straw shorteners, changes in sowing dates, varieties and fertilization, etc.) and climate change (lower precipitations and higher temperatures in temperate environment) may affect wheat height or growth as well as prey abundance, and therefore affecting Montagu's harrier fitness. Over the course of our study (16 years), available wheat heights have decreased overall and fluctuations of vole density have dampened (see Bretagnolle and Gillis 2010). These changes have apparently resulted in a relatively strong decrease of chosen wheat heights at the nest, suggesting that harriers currently do not nest in wheat fields of optimal heights. As a potential consequence, egg predation rate has been multiplied by 2.8 during the study period, and long-term persistence of the breeding harrier population is thus questioned in such farming habitat.

#### *Acknowledgements*

We thank Martine Guérif (INRA Avignon) for much help on wheat growth modelling. Many people helped collecting data in the field and are kindly thanked. We also thank Kévin Le Rest, Adrien Pinot and Vincent Lecoustre for helpful suggestions on statistical analyses. ANR BIODIVAGRIM and ANR-ERANET ECOCYLCES partly funded this study. HG was funded through a PhD from the ED "Diversité du Vivant", University of Paris VI.



**Appendix A**



*Inter-annual variations of wheat phenology index (1) and spring vole abundance index (2). The wheat phenology index was calculated from the annual wheat growth models as the mean annual julian date (from April 1<sup>st</sup>) necessary to wheat to reach the first quartile of absolute nest wheat heights (i.e. 70 cm). Spring vole abundance was estimated annually using line-trapping (see Salamolard et al. 2000 for more details).*



## **B.III. PATRONS TEMPORELS D'INSTALLATION DANS UNE COLONIE : L'IMPORTANCE DES VOISINS**

### **B.III.1. Résumé du chapitre**

Nous avons ici voulu approfondir l'étude de l'effet social détecté et exposé dans le chapitre précédent. Chez une espèce coloniale comme le Busard cendré, la compréhension des patrons temporels d'installation des individus est en effet cruciale afin d'appréhender la sélection d'habitat et pour promouvoir la mise en place de mesures de conservation adéquates. Certains auteurs (par exemple de Cornulier 2005, Cornulier and Bretagnolle 2006, Limiñana et al. 2011) vont même jusqu'à avancer que la sélection d'habitat basée sur la qualité intrinsèque de l'habitat physique jouerait un rôle mineur dans la distribution des espèces coloniales ou semi-coloniales, au profit du rôle majeur de l'attraction conspécifique. L'objectif principal de cette étude était donc de comprendre quels types d'information utilisent les couples de Busard cendré lors de leur installation selon leur rang d'arrivée dans la colonie. Notamment, utilisent-ils davantage une information personnelle basée sur leur capacité à distinguer la qualité des patchs d'habitat ou plutôt une information sociale, publique basée sur la présence de congénères (attraction conspécifique) ?

Devant la complexité de cette problématique, il paraît important de préciser nos hypothèses de travail. Ces dernières étaient les suivantes :

- Le premier couple s'installant dans une future colonie utilise exclusivement sa propre perception de la qualité de l'habitat (information personnelle) pour choisir le meilleur site
- L'utilisation de l'information sociale augmente avec le rang d'arrivée des couples suivants dans la colonie, au détriment de l'information personnelle
- Cette utilisation croissante de l'information sociale se traduit *in fine* par la sélection du même patch par tous les couples ou par l'utilisation par les nouveaux arrivants de patchs adjacents (de qualité) à ceux déjà occupés. Ces deux options sont modulées par la taille des patchs. En effet, si le patch est assez grand pour accueillir plusieurs couples tout en maintenant une distance raisonnable entre les couples (afin d'éviter la compétition inter-couple), le même patch pourra être utilisé. Dans le cas contraire, les derniers couples devront s'installer dans les patchs adjacents à celui ou



ceux occupés par les premiers couples afin de bénéficier des avantages de la colonialité.

Tout d'abord, précisons qu'un patch constituait, dans notre étude, une parcelle. Une fois la « future » colonie choisie (zone constituée de plusieurs parcelles), un couple arrivant a, en effet, le choix entre différentes parcelles de qualité variable (superficie, type de culture et surtout hauteur de végétation). Afin de tester les hypothèses énoncées, il nous fallait donc considérer seulement les individus coloniaux et échantillonner la qualité de chaque parcelle potentiellement favorable présente dans la colonie. Pour ce faire, nous devions définir une colonie. De façon basique, nous avons considéré les positions des colonies les années précédant notre étude pour délimiter nos zones. Dans celles-ci, la hauteur de végétation de chaque parcelle, favorable à la nidification du Busard cendré (céréales, luzerne ou ray-grass), a été mesurée chaque semaine entre fin avril et début juin (figure B.5), période d'installation des couples. L'ensemble de ces mesures a nécessité un investissement logistique considérable pour obtenir une taille d'échantillon acceptable (mais relativement faible). Le détail du protocole concernant le nombre de colonies étudiées, ainsi que le nombre de parcelles par année et par colonie, et enfin le nombre et la localisation des nids est précisé dans la section en anglais de ce chapitre.

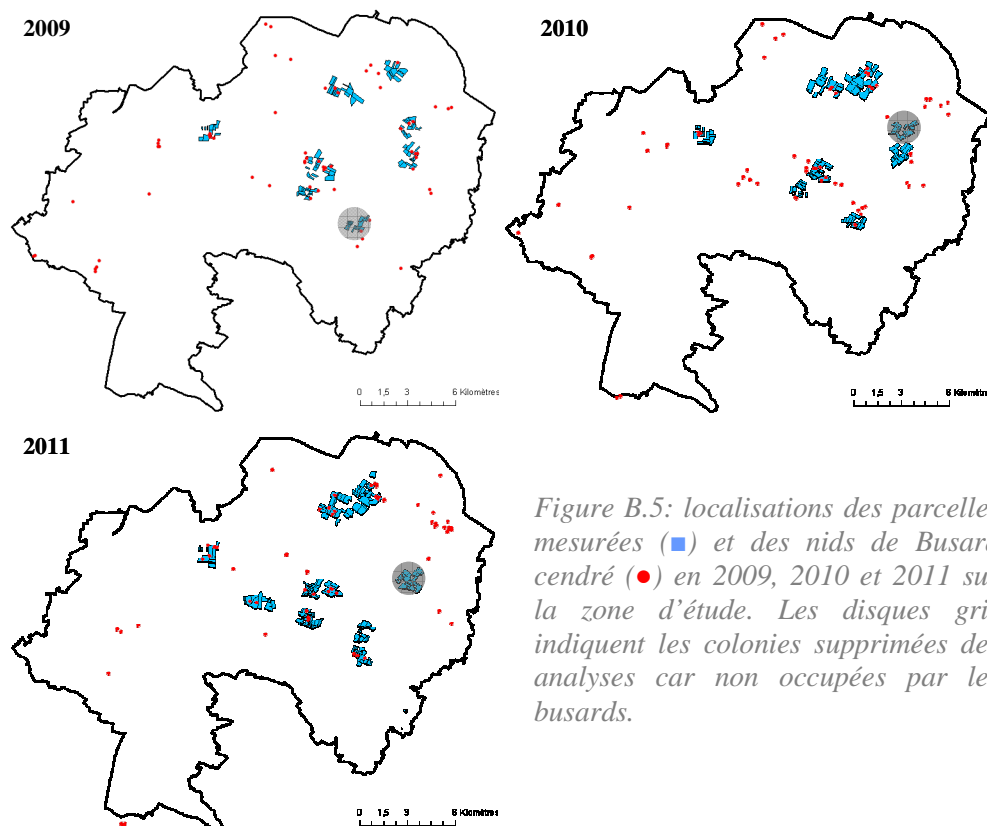


Figure B.5: localisations des parcelles mesurées (■) et des nids de Busard cendré (●) en 2009, 2010 et 2011 sur la zone d'étude. Les disques gris indiquent les colonies supprimées des analyses car non occupées par les busards.



Les résultats obtenus (détaillés dans la section en anglais) sont globalement en accord avec les hypothèses émises. Les premiers couples d'une colonie choisissent globalement les parcelles de qualité supérieure (en termes de hauteur de couvert). Les suivants, selon leur rang d'arrivée, semblent privilégier la proximité de congénères à la qualité relative des patchs. Cependant, une grande variabilité intra-rang dans l'utilisation de l'information a été mise en évidence. En effet, les individus d'un même rang semblent tantôt se baser sur leur information personnelle tantôt sur la présence des conspécifiques pour la sélection de leur patch de nidification. Ce patron répond au concept d'utilisation de l'information publique basée sur la présence de conspécifiques (« habitat copying », Valone 2007). Les couples d'un même rang s'installant dans des colonies différentes peuvent en effet avoir des capacités différentes de discernement de la qualité de l'habitat. Dans cette étude, cette capacité à discriminer la qualité d'un patch n'est que partiellement expliquée par la date de ponte relative des individus (proxy de la qualité). Cependant, elle doit également dépendre de l'expérience et l'âge des individus (non connus dans cette étude).

Cette étude nous apporte des éléments essentiels quant au rôle de l'attraction conspécifique dans la sélection d'habitat chez une espèce semi-coloniale telle que le Busard cendré. La connaissance et la prise en compte de ces éléments est indispensable dans la mise en place de mesures de conservation de l'espèce, et ce d'autant plus dans un contexte de changement global où la qualité des patchs (hauteur du couvert) est en diminution (mis en évidence dans le chapitre précédent). Après avoir étudié les patrons d'installation des couples au sein d'une même colonie, nous pouvons, à présent, nous poser la question du choix même des colonies. En effet l'emplacement des colonies est relativement stable d'une année sur l'autre et semble être influencé par le choix des couples précoces. Mais le choix fait par les couples de retourner dans la même zone d'une année à l'autre est-il influencé par le succès de cette colonie au cours des années précédentes, lui-même du à une qualité globale supérieure de cette zone par rapport aux autres secteurs disponibles? C'est la question à laquelle nous tentons de répondre dans le chapitre suivant.



### ***B.III.2. article 3***

**Is there a balance between physical and social cues for nesting habitat choice in a facultative colonial breeder?**

**H. GILLIS\* and V. BRETAGNOLLE**

CNRS-UPR 1934, Centre d'Etudes Biologiques de Chizé, 79360, Beauvoir sur Niort, France

\*Corresponding author : Hanneke Gillis

E mail: [gillis@cebc.cnrs.fr](mailto:gillis@cebc.cnrs.fr); [hanneke.gillis@yahoo.fr](mailto:hanneke.gillis@yahoo.fr)

Article en préparation



### *Summary*

Most species face a heterogeneous environment and have therefore to collect information about the relative quality of habitat patches before selecting one for breeding. When selecting a breeding site, individuals can use two main sources of information to assess breeding patch quality: personal information or public information. Personal information is often favoured when individuals are able to discriminate patch quality. Public information is used to reduce costs associated with patch quality assessment or when individuals are not able to assess this quality. It is based on presence or success of conspecifics. Here, we investigated field (i.e. patch) selection in nesting colonies of Montagu's harrier in a farmland area according to field quality, to conspecifics presence and to pair arrival rank in the colonies. We found that first pairs in each colony overall selected for the best quality patches (i.e. based on personal information) but this selection overall decreased with pair rank in the colony at the same time that the importance of conspecific presence (i.e. public information) increased. For pairs of a same rank, we found some variations in relative selection and in the kind of information used. This underlined that personal information could enter in conflict with public information and that individuals have to deal with a trade-off between costs and benefits of coloniality leading to different decisions according to pair harrier quality and ability (i.e. pair experience, age, etc.) to discriminate patch quality. Conflicts of public and personal information and potential trade-off between costs and benefits of coloniality were further discussed to explain the observed semi-coloniality in this species.



## ***Introduction***

Animals have to make many choices to maximize their fitness among which selecting foraging or breeding habitats (Danchin et al. 2004). The selection of a particular habitat, shaped by natural selection (Southwood 1977, Clark and Shutler 1999), leads to non-random distributions of animals among habitats (Southwood 1977, Burger 1987, Clark and Shutler 1999, Kolbe and Janzen 2002). Most species face a spatially and temporally heterogeneous environment (Danchin et al. 1998) and thus have to collect information about the relative quality of habitat patches before selecting one for breeding or foraging (Wiens 1976, Danchin and Wagner 1997, Danchin et al. 1998, Danchin et al. 2004). In an Ideal Free Distribution situation, individuals should distribute themselves among patches according to their quality and to conspecific density (Fretwell and Lucas 1969). However, some kind of social cues could lead to skewed distributions (Wagner and Danchin 2003) with more or less individuals in a patch than expected according to its quality (Danchin and Wagner 1997), leading for instance to Ideal Despotic Distribution (review in Sutherland 1996). These social cues are likely leading to animal aggregations and are therefore regarded as potential hypotheses that could explain colony formation (Danchin and Wagner 1997).

When selecting a breeding site, individuals can use two main sources of information to assess breeding patch quality (Valone 2007). On one hand, an individual could directly sample information by estimating a variety of parameters that relate to physical (altitude, temperature, humidity and vegetation structure) or biological (prey, predator and parasite abundances) habitat features (Valone 2007). However, this personal mean of acquiring information requires time and energy, hence increasing individual costs (Valone 2007). To limit these costs, an individual could alternatively (or additionally) use social information (Danchin et al. 2004, Valone 2007). In habitat selection, this social information involves two main kinds of cues: the presence and behavioural decisions of conspecifics, and the breeding success of conspecifics ("Public Information", PI, Danchin and Wagner 1997, Danchin et al. 2004). These cues are often provided inadvertently ("inadvertent social information", ISI, Danchin et al. 2004). Many studies, performed on various animal taxa, have demonstrated the influence of ISI on breeding habitat selection (Danchin and Wagner 1997, Parejo et al. 2007, Valone 2007).

Agricultural landscapes are interesting since landscape changes from year to year (because of crop rotation), therefore reducing temporal autocorrelation in habitat quality.





Therefore, public information based on breeding performance previous year may not be reliable one year to another at least at a small scale. Information based on presence and behavioural decisions of conspecifics, commonly called “habitat copying” (Danchin et al. 1998), should therefore be involved in small scale habitat selection. This copying behaviour implies conspecific attraction leading an individual to settle near others (Danchin et al. 1998, Wagner and Danchin 2003, Valone 2007). This behaviour could be explained by i) reduced search costs of the imitator (i.e. “local enhancement; Kiester 1979, Stamps 1988, Greene and Stamps 2001, Valone 2007), ii) providing benefits (i.e. reduced predation risk, increased ability to deter intruders and increase access to mates) to the imitator (Stamps 1988, Valone 2007) and/or iii) providing information on habitat quality (Wagner and Danchin 2003, Valone 2007). The distinction between these three explanations is not obvious since they are non exclusive (Valone 2007). It is further unclear that habitat copying is a source of PI to assess habitat patch quality (Valone 2007). Actually, it depends on relative habitat quality of patches and on the ability of an individual to discriminate patches according to their quality (Nordell and Valone 1998, Valone 2007). Individuals able to differentiate the quality of patches should exhibit habitat copying only if the best patch is already occupied, otherwise they should occupy the best patch and thus not copy (Nordell and Valone 1998, Valone 2007). On the other hand, an individual unable to assess the respective quality of patches (i.e. often young and poor quality individuals, Valone 2007) should select randomly or perform habitat copying to enhance its chance to breed in a high quality patch (Nordell and Valone 1998, Valone 2007). The presence of conspecifics may however not always be a good proxy of patch quality: if previously settled individuals are not able to discriminate patch quality, habitat copying could lead to a misleading selection.

Here we studied the temporal pattern of installation in a colony (i.e. small scale habitat selection) of a semi-colonial ground-nesting bird, the Montagu’s harrier *Circus pygargus*, breeding in a high changing environment both temporally and spatially, i.e. an intensive agricultural landscape. Ground-nesters breeding in such a landscape will thus have the choice among fields to breed. The study species breeds in loose colonies and nests mainly in winter cereal crops in Western Europe (but also in alfalfa and ray-grass; Cramp and Simmons 1980). Several studies already mentioned the importance of vegetation height for determining nest location (Limiñana et al. 2006, Limiñana et al. 2011). Fields with tall vegetation could therefore be considered of higher quality. This particular study species and its breeding habitat appear ideal to test empirically the hypothesis of Nordell and Valone (1998) that



Montagu's harrier use habitat copying in a PI sense to select a field to breed. To do so, we investigated the intra-colony choice of a field by successive breeders according to crop type, crop height, field size, laying date and the potential modulation of choice by conspecifics presence. We predict that first pairs of each colony will chose the best quality field (i.e. highest vegetation) based on their personal information while the followings will be based more and more on PI (i.e. habitat copying) to select their nesting field according to their rank of arrival on the colony.

### *Materials and methods*

#### Study area and species

Montagu's harriers *Circus pygargus* have been monitored since 1995 in the *Zone Atelier Plaine et Val de Sèvre*. This intensively managed farmland landscape is located in central-western France (Deux-Sèvres: 46°11'N, 0°28'W). It covers 450 km<sup>2</sup>, and crops are dominated by cereals (40% of total surface), colza and spring-sown crops (maize, sunflower and pea). Since 1994, land-use has been monitored and classified in the field each year and incorporated in a Geographical Information System. This particular landscape consists in many fields that could be regarded as different relative small habitat patches of different qualities according to their crop type, vegetation density and height.

The Montagu's harrier is a trans-saharan migratory raptor, breeding in Europe and Asia. In Western Europe, nests are found within crops, mainly in winter cereal fields (wheat and barley) and rye-grass or alfalfa (Cramp and Simmons 1980). Nowadays, cereal crops seem to be the most frequent breeding habitat of this species in France (70 % of nests; Arroyo et al. 2002). Nest vegetation height is critical in determining its nest location (Arroyo et al. 2004, Limiñana et al. 2006, Limiñana et al. 2011, Gillis et al.[b] in review). Indeed, among cereals fields of a large scale region (e.g. our study area), harriers overall choose higher cereal fields to breed (Gillis et al.[b] in review) because high vegetation has the potential to provide nest protection against predation and overheating (Gillis et al. [a] in review). Fields with high vegetation height seems thus to be of better quality, at least in cereals.

In addition, this species breeds semi-colonially (facultative coloniality): some nests are isolated, but most (80-85% in France and Spain) are found in small colonies of 2-30 pairs (Arroyo et al. 2002, Arroyo et al. 2004). In our study site, distance between nests within colonies is on average  $155 \pm 137$  m ( $n = 461$ ) and average number of neighbours was  $5.8 \pm$



5.4 pairs with a maximum of 21 pairs (Arroyo et al. 2004). In western France, aggregation seems to be food depend in this species, with more aggregation (i.e. more nests in colonies and thus less isolated nests) in years of high abundance of Common vole *Microtus arvalis*, its main prey over our study area (Arroyo et al. 2004). In successive years, colony positions are globally maintained though individuals may shift of colony from year to year (Arroyo et al. 2004). In our area, colony distributions seem to be dependent on food abundance and breeding success in previous years (i.e. colonies with higher success one year are more likely to welcome breeders next years) suggesting that Public information based on conspecifics success may be used. Additionally, Arroyo et al. 2004 suggested that temporal settling patterns appear to be influenced by presence of conspecifics, since late breeders tend to install in occupied areas.

#### Data collection

Data were collected during the springs of 2009, 2010 and 2011. Over the study area, we restricted our data collection to particular areas corresponding to high harrier nest densities (i.e. colonies) in previous years. We thus defined 24 areas (8 per year). Their positions were in most cases the same every year, but one colony was removed and replaced by another one in 2011. In each area, from end April (i.e. before harrier laying) to beginning June (i.e. at the end of wheat growth), we weekly measured vegetation heights of each field with *a priori* favourable crop type for harrier nesting (i.e. wheat, barley, alfalfa and rye-grass). At total of 393 fields were measured to the nearest 5-centimetres over the 3 years (n = 106 in 2009, 139 in 2010 and 148 in 2011). Number of fields per area varied from 10 to 24 (mean  $\pm$  standard deviation:  $15.6 \pm 3.9$ ). Additionally, over the sampling period, some alfalfa or rye-grass fields were progressively excluded of the measured sample because of mowing events (i.e., fields became unavailable for breeding harriers). Obviously, because of crop rotation, sampled fields partly differ year to year even if area location was the same. Since agricultural landscape facilitates vegetation structure metrics (intra-field vegetation height homogeneity) compared to a natural environment, only one measurement per field was performed each time.

Over the entire study area, nests were located each year according to standardized effort. Nests were visited as early as possible and afterward regularly checked to collect data on laying date, clutch size, hatching success, fledging success, predation events and nest vegetation height at visit date. Laying date was directly estimated for some nests visited during laying or by backdating from hatching date (i.e., incubation duration, 29 days, was



subtracted from hatching date). Hatching was directly dated from visits at hatching time or assessed from chick and/or egg measurements (Millon et al. 2002). Only nests present in our areas (i.e. in the measured fields) or in the direct periphery of them (i.e. in an unmeasured field near a measured one) were conserved for our study. Some nests however came from unmeasured fields: in those cases we were able to calculate vegetation height at any date based on nest vegetation height measured at visit date and crop growth modelling (see Gillis et al. [b] in review for method). For each nest, vegetation height of chosen field and of all available fields were measured or assessed at week of laying.

### Statistical analysis

We investigated field selection of first, second and third pairs installed in each colony by using generalized linear mixed-effects models. Year (three levels) and colony identity (9 levels) were included as random effects since some differences in selection among years could occur according to food abundance and crop phenology variations (Gillis et al. [b] in review) and since uncontrolled among-colony differences apart from differences in range of vegetation heights were expected. The response variable of all models was the probability of a field to be selected by a harrier (binomial error distribution with a logit link). For all models performed, we limited explanatory variables to those investigating *a priori* hypotheses. We then performed a backward procedure based on p-values to keep and present only significant effects.

We first investigated field selection for each rank (i.e. 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup>) according to “field quality”. We assumed that field quality depends on 3 variables: field surface (a continuous variable expressed in ha), crop type (a two level factor: grassland, i.e. alfalfa and rye-grass; and cereals, i.e. wheat or barley) and relative vegetation height (a continuous variable expressed in cm) and the interaction of these two last variables. We used relative field height (field height – mean of heights of all fields per crop of a colony) instead of absolute field height to blur potential differences in range of available heights among colonies and years. As a second step, for second and third pairs, we kept only significant effects of previous model (i.e. “field quality” model) and added social variables: presence of conspecifics (a two level factor: presence or absence) and its interactions with field surface and relative field vegetation height. We then compared AIC values of the “field quality” and the “social” models to examine if adding social information improved the model. Once patterns were highlighted, we tried to explain them by exploring the effect of pair quality (i.e.



relative laying date). Additionally, we investigated whenever pair rank influenced the selection for a particular vegetation height and the minimal distance between target pair and the nearest neighbour. We therefore performed linear models (identity link).

Statistical procedures were performed using R (version 2.12.1, R Development Core Team, 2010). Descriptive statistics are expressed as mean  $\pm$  standard deviation.

### **Results**

Over the three years, 3 of the 24 *a priori* defined areas (one per year) were not selected by breeding harriers, and were thus excluded from analysis. The remaining areas supported a total of 90 nests (N = 31 in 2009, 28 in 2010 and 31 in 2010). 73 nests (80 %) were located in wheat, 12 in alfalfa (13.3 %) and 6 in barley (6.7 %). Colony size varied from 2 to 10 nests with an average of 5.3 nests within each colony. In 12 areas (57 %), at least one occupied (by breeding harrier) but unmeasured field was added, usually a field at the periphery of the *a priori* defined area.

#### First settled pair

Laying date of the first pair in each area\*year ranged from April 23<sup>rd</sup> to May 26<sup>th</sup> (mean:  $34.2 \pm 7.9$  Julian days). In six colonies (29 %, 4 in 2009 and 2 in 2010), the first pair chose to nest in alfalfa. In all other colonies (15, i.e. 71%), they selected cereal fields (i.e. wheat for 14 colonies but barley for 1 colony in 2011). The first pairs chose to nest in the highest cereal field available among those available in 4 colonies, and in the highest alfalfa field in two further colonies; therefore, in two third of the colonies, the first pair did not settle in the tallest field. Selection for height in cereals was significant, which was not the case for alfalfa (Table 1, Fig. 1b). Interestingly, relative laying date of first pairs breeding in alfalfa was  $-14.3 \pm 5.1$  days, compared to  $-7.2 \pm 8.23$  for those breeding in cereals. The difference was significant, (Fig. 1c, t-test:  $t = 2.37$ ,  $p = 0.03$ ), possibly suggesting that pairs setting in alfalfa, which were less selective relative to vegetation height than those setting in cereals, were likely of better quality (i.e. breeding very early in a season). The first pair also chose preferentially larger fields (Table 1, Fig.1a), both in wheat and alfalfa (Table 1).



Table 1: Mixed model investigating nest field selection of first pair installed in each colony. Year and colony identity were treated as random factors. Num df and Den df represent the numerator and denominator degrees of freedom, respectively

	Num df	Dem df	Chi	P
Intercept	1	338	58.10	<0.001***
Relative field height	1	338	7.16	0.007**
Crop type	1	2	12.23	<0.001***
Field surface	1	338	4.06	0.04*
Relative field height × crop type	1	338	3.16	0.07.

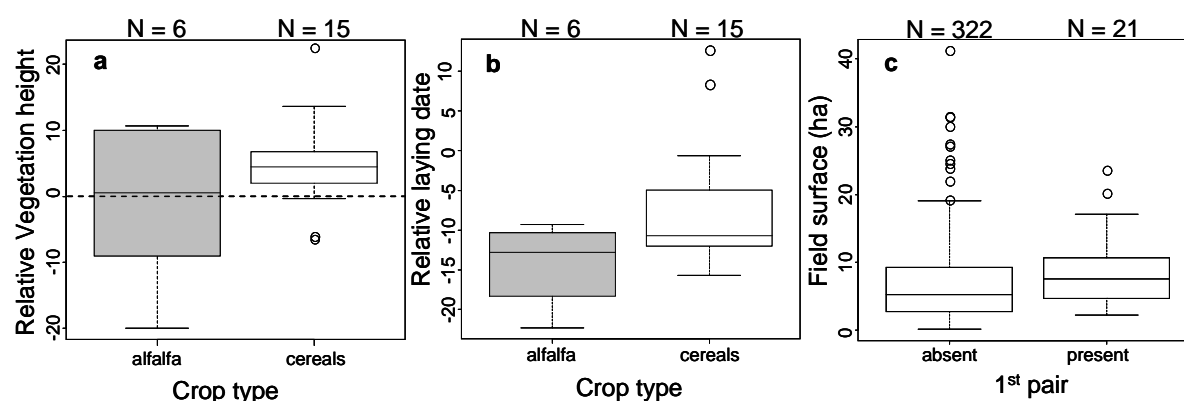


Figure 1: Field selection by first pair installed in the colony: (a) difference in relative vegetation height of alfalfa and cereal chosen by first pair; (b) relative laying date (i.e. pair quality) difference between first pairs that chose alfalfa or cereals to nest; (c) Field surface difference between fields chosen or not by first pairs.

### Second settled pair

Second pairs settled in colonies laid eggs from April 25<sup>th</sup> to June 6<sup>th</sup> (average  $41 \pm 10$  Julian days), laying on average  $6.73 \pm 6.07$  days after first pairs. In two colonies, two pairs laid at the same date leading to a total of 23 second pairs for 21 colonies. Only two pairs laid in alfalfa (8.7 %) while all others laid in cereals (91.3 %). In sharp contrast to first settled pairs, second pairs did not prefer alfalfa (no effect of crop type, Table 2a). They selected larger fields (Table 2a, fig. 2a), and showed more positive selection to vegetation height than first pairs, in each colony whatever crop type (Table 2a, Fig. 2b). Five and one second pairs respectively nested in the highest wheat and alfalfa fields.

In addition, the presence of the first pair enhanced the probability of a field to be occupied (i.e. AIC was improved between models of Table 2a & 2b:  $\Delta AIC = 4.9$ , Fig. 2c). Indeed, 6 second pairs were in the same field as first pairs (26.1%). Fields selected by both the first and the second pair were larger than those selected by the first pair only ( $t = -2.15$ , df



= 21, p-value = 0.04; Fig. 2d). Seven second pairs laid in a field with lower vegetation height than first pairs (30.4%, Fig 3a & b) suggesting they were less selective with regard to vegetation height while in the same time they were not choosing to nest in the same field as first pairs. Furthermore, among them, 4 laid in lower plots than the average of each colony (hatched area in Fig. 3a) suggesting they were neither able to discriminate field quality nor to perform habitat copying. The 3 others pairs nesting in lower plot than first pair chose higher fields than available on average (dark grey area in Fig. 3a) suggesting they still selected a field of suitable quality. Ten pairs chose to lay in a taller field (43.5%) than the first pair (light grey and white areas in Fig. 3a) suggesting they based their choice rather on personal information. At the laying date of second pair, field height difference between 1<sup>st</sup> & 2<sup>nd</sup> pair actually decreased with absolute field height of 1<sup>st</sup> pair (Pearson correlation:  $r = -0.48$ , p-value = 0.02, Fig. 3b) suggesting that when 1<sup>st</sup> pair chose low vegetation height (i.e. alfalfa or low wheat), the 2<sup>nd</sup> pair tended to select in favour of very high vegetation fields (Fig. 3b). Pair quality (i.e. measured by the proxy of relative laying date) did not explain field height difference between 1<sup>st</sup> & 2<sup>nd</sup> pair ( $r = -0.24$ ,  $p = 0.28$ ).

Table 2: Mixed model investigating nest field selection of second pair installed in each colony. Year and colony identity were treated as random factors. Num df and Den df represent the numerator and denominator degrees of freedom, respectively. a) Model based on habitat quality alone, b) model based on habitat quality and social information

a)

	Num Df	Dem Df	Chi	P	AIC
Intercept	1	362	66.60	<0.001***	154.6
Relative field height	1	362	23.64	<0.001***	
Field surface	1	362	6.40	0.01*	

b)

	Num Df	Dem Df	Chi	P	AIC
Intercept	1	362	65.60	<0.001***	149.7
Relative field height	1	362	22.04	<0.001***	
1 <sup>st</sup> pair presence	1	2	8.11	0.004**	
Field surface	1	362	4.75	0.03*	

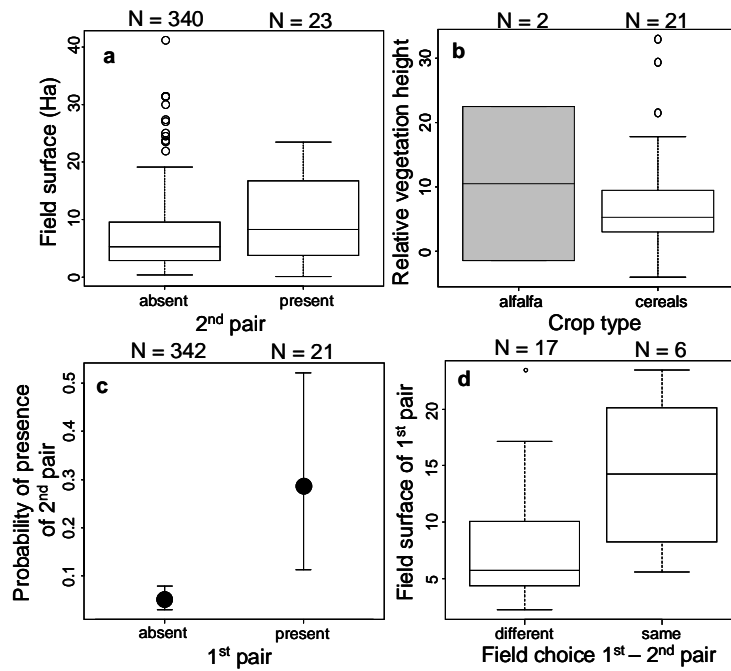


Figure 2: Field selection by second pair installed in the colony: (a) Field surface difference between fields chosen or not by second pairs; (b) relative vegetation height of chosen fields by second pair according to crop type; (c) probability of second pair presence according to first pair occupancy and; (d) differences of field surface between fields welcoming the first pair and those welcoming both first and second pairs.

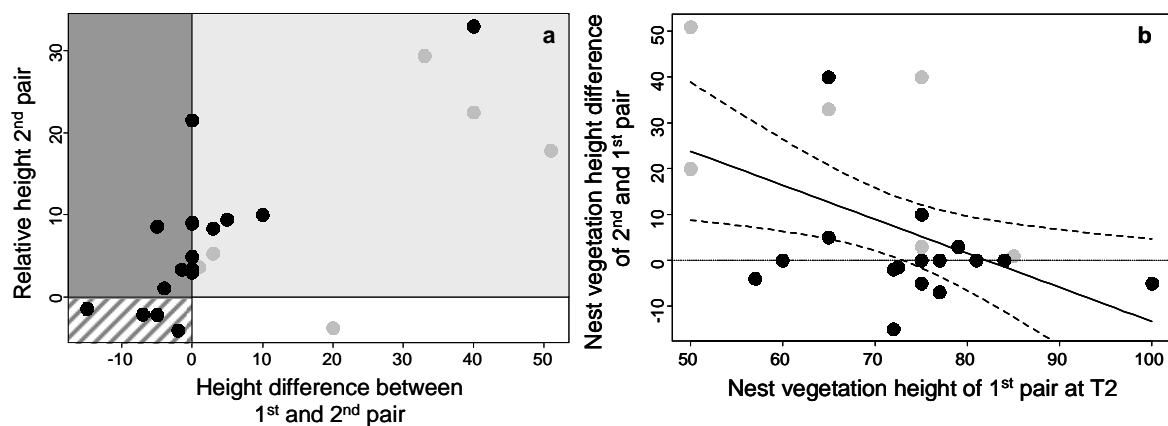


Figure 3: Comparison of chosen fields by first and second pairs: (a) Relative height of field chosen by second pair as a function of height difference between fields chosen by first and second pair and (b) Field vegetation height difference between first and second pair as a function of vegetation height of field chosen by first pair at the date of laying of second pair. Grey dots (●) and black dots (●) represent colonies in which first pair chose alfalfa and cereals respectively. In (a), pairs placed above the horizontal line selected higher fields than available (light and dark grey areas). Those placed under this line (hatched and white areas) selected lower fields than available on average (i.e. poor-quality pairs). Pairs placed at the left of the vertical line (hatched and dark grey areas) select for lower fields than first pairs and the reverse is true for those placed at the right of the line (light grey and white areas). Pairs on the vertical line were in the same field than first pairs.

### Third settled pairs

Three colonies had only two pairs leading to a total of 18 colonies that had a third pair, but in one colony, two pairs laid at the same date leading to a total of 19 third pairs. Third pairs laid from April 27<sup>th</sup> to June 1<sup>st</sup> (mean:  $47 \pm 10$  Julian days). They laid on average  $9 \pm 7$  days later than second pairs and  $14 \pm 9$  days later than first pairs. Two of these pairs laid in





alfalfa while all others chose cereals. The probability of a field to be occupied by the third pair was not affected by field quality, i.e. relative vegetation height, crop type and field surface (see table 3). Three third pairs chose to nest in a field already occupied by the first pair installed and for two of them it was also the field chosen by the second pair (Fig. 4). Four third pairs laid in higher fields than first pairs (at the date of laying of third pair, light grey area in Fig. 4a) and three in higher fields than second pairs (light grey area in Fig. 4b) suggesting they based their choice on personal information. 8 and 11 third pairs respectively installed in lower than first and second pairs (dark grey and hatched areas in Fig. 4a & b). In contrast with second pairs, more pairs laid both in lower fields than the two first pairs and in lower fields than the average of each colony (hatched areas in Fig. 4a & b) suggesting that more third pairs than second ones were unable to discriminate field quality and nest in the same field than the first or second pair. These pairs might be attracted by first or second pair but were unable to nest in the same plot because of small field surfaces. Indeed, the probability of a field to be occupied is enhanced when the field already welcomed a pair and was large enough to welcome another one (Tab. 3, Fig. 5). At the laying date of third pair, field height differences between 1<sup>st</sup> & 3<sup>rd</sup> pair or 2<sup>nd</sup> & 3<sup>rd</sup> pair actually decreased with absolute field height of 1<sup>st</sup> pair and 2<sup>nd</sup> pair respectively (1<sup>st</sup> pair,  $r = -0.61$ ,  $p\text{-value} = 0.01$  ; 2<sup>nd</sup> pair,  $r = -0.69$ ,  $p\text{-value} = 0.003$  ; Fig. 4c & d) suggesting that pairs selecting high vegetation did it when previous pairs nested in low vegetation. We found a slight effect of pair quality (i.e. relative laying date) on field height difference between 1<sup>st</sup> & 3<sup>rd</sup> pair ( $r = -0.47$ ,  $p\text{-value} = 0.04$ ): the later third pairs in comparison with first pair, the less they are selective according to vegetation height.

*Table 3: Mixed model investigating nest field selection of third pair installed in each colony. Year and colony identity were treated as random factors. Num df and Den df represent the numerator and denominator degrees of freedom, respectively. Simple effects involved in the interesting interaction were kept in the model even if not significant.*

	<b>Num Df</b>	<b>Dem Df</b>	<b>Chi</b>	<b>P</b>
Intercept	1	284	28.55	<0.001***
1 <sup>st</sup> or 2 <sup>nd</sup> pair presence	1	2	1.03	0.31
Field surface	1	284	0.41	0.52
1 <sup>st</sup> or 2 <sup>nd</sup> pair presence × Field surface	1	284	3.07	0.07

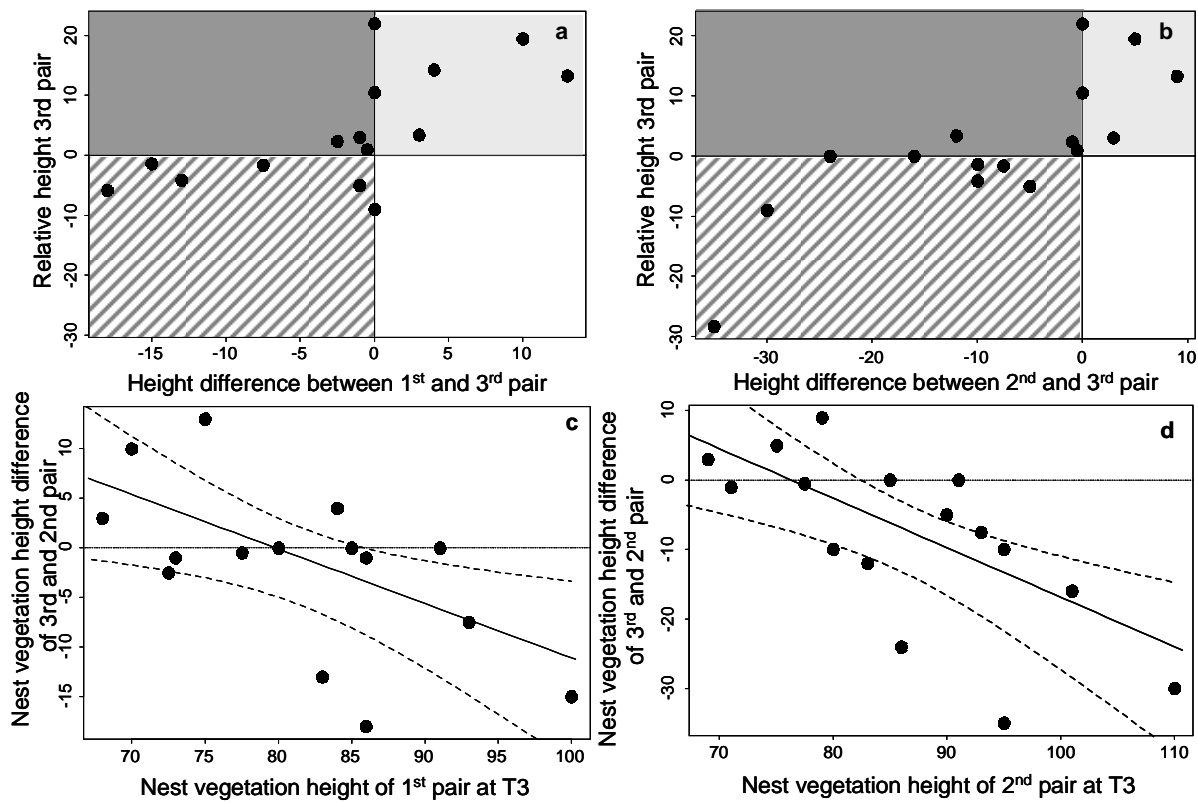


Figure 4: Comparison of chosen fields by first, second and third pairs: Relative height of field chosen by third pair as a function of height difference between fields chosen by first and third pair (a) and by second and third pair (b) Field vegetation height difference between first and third pair (c) and second and third pair (d) as a function of vegetation height of field chosen by first pair (c) and second pair (d) at the date of laying of first (c) and second pair (d). In (a) & (b), pairs placed above the horizontal line selected higher fields than available (light and dark grey areas). Those placed under this line (hatched and white areas) selected lower fields than available on average (i.e. poor-quality pairs). Pairs placed at the left of the vertical line (hatched and dark grey areas) select for lower fields than first pairs (a) or second pairs (b) and the reverse is true for those placed at the right of the line (light grey and white areas). Pairs on the vertical line were in the same field than first pairs (a) or second pairs (b).

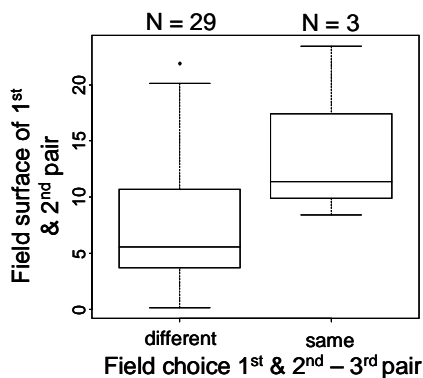


Figure 5: Differences of field surface between fields welcoming the first pair and/or the second one and those welcoming the three first pairs.

Overall, relative vegetation height at nest (i.e. selection according to vegetation height) tended to decrease with pair rank in the colony (coefficient estimate = -0.95, p-value = 0.08; Fig. 6a) suggesting that last breeders arriving on colonies were less selective than first ones.



Furthermore, the distance of nearest neighbour decreased with pair rank (coefficient estimate = -0.17, p-value = 0.006; Fig. 6b). Attraction therefore occurred.

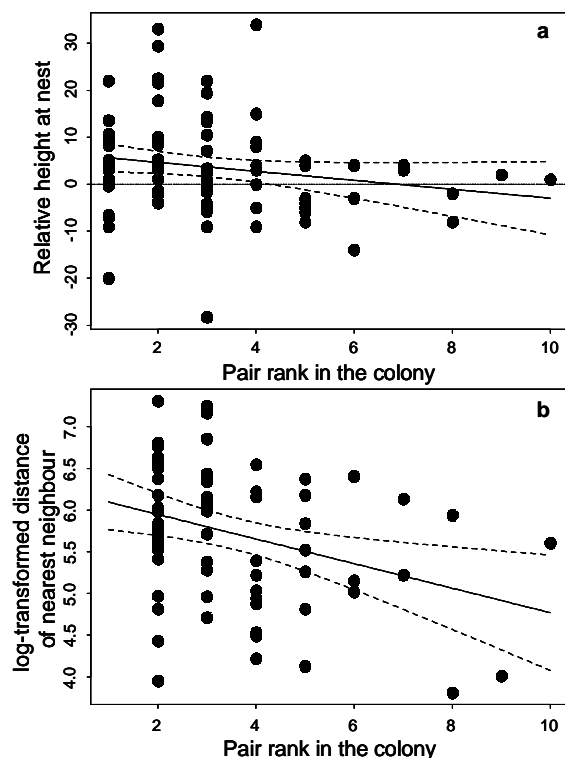


Figure 6: Relative height of chosen field (a) and log-transformed distance of first neighbour (b) as a function of pair rank in the colony.

### Discussion

In this study, we analysed how individuals make settlement decisions according to neighbourhood and patch quality. We showed that in Montagu's harriers, patch selection for nesting is a conditional strategy that depends on patch quality but also on conspecific presence, the relative balance between the two cues depending on pair rank within the colony. First pairs selection was indeed based only on patch quality (i.e. personal information), but this selection decreased with pair rank in the colony at the same time that the importance of conspecific presence (i.e. PI) increased. As a consequence, pairs arriving last in a colony tend to be less selective on patch quality and nest closer to a neighbour than previous pairs. Imitating the choice of conspecifics is for last breeders a way to make better decisions when they lack personal information (Nordell and Valone 1998, Wagner and Danchin 2003). This pattern must be the result of the decrease of pair ability to assess patch quality with their relative arrival date in the colony. Additionally, late breeders (i.e. poor-quality breeders) may acquire some advantages to nest close to early breeders (i.e. high-quality breeders) including the opportunity for extra-pair copulation (Velando and Freire 2001). Montagu's harrier is a migratory species and is therefore prone to use PI because they are limited in time to assess



patch quality (Parejo et al. 2007). Global patterns are thus consistent with our initial hypotheses. However, strong variations in information use and thus selection were observed for individuals of a same arrival rank.

First pairs installed in colonies could only base their field selection on personal information or on experience. However, they were not always found to nest in tallest vegetation. Earliest pairs known as of better quality even settled in low alfalfa suggesting that due to their high quality they are able to face higher predation risk. Alternatively, alfalfa in early season could provide a high concealment level compared to cereals because of denser cover. First pairs, interestingly, selected for large fields. Two not mutually exclusive hypotheses could be formulated to explain this pattern. On one hand, nesting in a large uniform patch may decrease predator search efficiency. On the other hand, first pairs may favour large fields to enhance the probability of welcoming neighbours and thus increase conspecific cooperation for mobbing predators (Arroyo et al. 2001). This last hypothesis would imply that first pairs produce a sort of intentional information to attract conspecifics.

Second pairs setting in colonies were still of high quality and thus partly based their nest site selection on personal information but this pattern was attenuated with rank increase (i.e. third pairs). Actually, pairs did so when previous pairs laid in low wheat or in alfalfa. This reflects a rapidly changing environment where the use of the presence of conspecifics is not favoured (Danchin and Wagner 1997): Alfalfa is suitable early in season but its relative quality (compared with cereals) deteriorates with time. In this species, PI is thus not always reliable since environment is changing rapidly (Parejo et al. 2007). However, PI might be used by some pairs laying in the same field or in lower fields than previous pairs and than available on average. If pairs nested in the same field than previous ones but that these previous pairs laid in lower fields than available, “blind” habitat copying should have occurred (Valone and Templeton 2002, Wagner and Danchin 2003). It was rarely the case in our study (only one third pair exhibit such a choice). Therefore, we could not absolutely discriminate personal or PI use. On another hand, individuals selecting lower fields than previous pairs and than available (a proportion that increased with pair rank) may not be able to assess patch quality and we believed they did not perform habitat copying (i.e. nest in the same field as first pair) because of the existence of intraspecific competition in space. Indeed, they might be attracted by previous pairs but the occupied field might be too small to welcome a second pair. They therefore tend to lay closer to conspecifics (i.e. in an adjacent field whatever its height) to deal with the trade-off between the benefits (i.e. reduced predation risk, Arroyo et al. 2001) and the



costs of coloniality (i.e. competition for food, mates; Arroyo et al. 1995, Arroyo 1999, Mougeot et al. 2001, Arroyo et al. 2001). We found no consensus in strategy used by pairs of a same rank: some used personal information while others seemed to relate to PI. However, public information based on conspecifics decisions (i.e. for habitat copying) predicts this kind of pattern when individuals differ in their ability to discriminate patch quality (Valone 2007) or differ in their quality. Pairs arriving in an occupied area can obtained both PI and personal information and seemed to rely on public information when many pairs are already installed. In this framework, individuals prefer relying on PI because they are late breeders (i.e. often young and of poor quality, Valone 2007) with an unreliable personal information (Coolen et al. 2003, Van Bergen et al. 2004, Valone 2007). On the other hand, harriers arriving in an area with few conspecifics already installed (i.e., one or two) could often rely on their personal private information because of their relative good quality. This personal information could enter in conflict with public information (Van Bergen et al. 2004, Valone 2007) leading different decisions (based on PI or personal information) according to harrier relative assessment ability (Valone 2007). In our study, we did not really succeed in relying decisions to pair quality (i.e. relative laying date). We were certainly missing some information about relative pair quality such experience and age of pairs of a same rank.

Montagu's harrier is a semi-colonial species that may breed both solitarily and in colonies of different sizes. At a large spatial scale, conflicts of PI and personal information leading to difference in information individuals lay on to select their nest site, may be a hypothesis to explain the observed semi-coloniality in such a species. Additionally, depending on their phenotype, individuals must balance the trade-off between costs and benefits of coloniality leading to solitary and colonial individuals. Here, we highlighted the importance of social (i.e. presence of conspecifics) and physical (i.e. field quality) components of habitat on nest site selection at the small scale that constitutes a colony. Colonies placement seems thus to be dependant on first pair installed. A further step will be to investigate colonies position according to large patch quality or public information based on breeding success previous year.

### *Acknowledgements*

Many people helped collecting data in the field and are kindly thanked. We also thank Kévin Le Rest, Matthieu Authier and Paul Miguet for helpful suggestions on statistical analyses.



ANR BIODIVAGRIM and ANR-ERANET ECOCYLCES partly funded this study. HG was funded through a PhD from the ED “Diversité du Vivant”, University of Paris VI.

## **B.IV. ETUDE DE LA SELECTION D'HABITAT A** **DIFFERENTES ECHELLES SPATIO-TEMPORELLES**

### ***B.IV.1. résumé du chapitre***

Les chapitres précédents soulignent que la sélection du site de nidification du Busard cendré est largement dépendante de la hauteur du couvert. Cependant, il s'agit d'un processus complexe influencé par l'ensemble des composantes de l'habitat (physique, biologique et sociale) et pouvant impliquer diverses échelles spatiales et temporelles. Dans cette partie, nous abordons l'effet de la répartition des habitats physiques favorables (au regard de la structure de la végétation) sur la localisation des nids à plusieurs échelles spatio-temporelles. Pour cela, nous nous sommes posé deux grandes questions :

- Existe-t-il une structure spatio-temporelle des habitats physiques favorables à l'échelle de la zone d'étude ?
- Cette structure spatiale explique-t-elle la position des nids à l'échelle de la zone d'étude et à des échelles plus locales ?

Pour répondre à ces questions, des données de qualité d'habitat sur l'ensemble de la zone d'étude et sur plusieurs années sont nécessaires mais logistiquement difficiles à récolter sur le terrain. Pour remédier à ce problème : nous nous sommes focalisé sur les nids localisés dans le blé uniquement (près de 80% du nombre total de nids) et nous avons utilisé des indicateurs phénologiques du blé provenant de la télédétection afin d'acquérir des données d'habitat couvrant une proportion maximale de la surface de la zone d'étude sur une large échelle de temps. L'obtention de ces données d'habitat fut possible grâce à une collaboration étroite avec des chercheurs et ingénieurs de l'équipe EMMAH de l'INRA d'Avignon. Leur expertise en termes de mise au point de méthodes de caractérisation du milieu, notamment grâce à la télédétection, nous a en effet permis d'avoir des données de qualité de blé (indice de précocité, utilisé comme proxy de la hauteur du blé) à l'échelle de pixels de 250m (résolution des images MODIS utilisées) sur une période de 10 ans (2001-2010). Les méthodes utilisées pour l'estimation de cet indice de précocité du blé sont étayées dans l'article issu de ce chapitre.

Pour l'étude de la sélection d'habitat à large échelle (échelle de la zone d'étude, 460km<sup>2</sup>), nous avons examiné la densité de nids par pixel en fonction de la précocité estimée

du blé. Afin de tester la sélection d'un pixel, pour la nidification, à des échelles plus restreintes, différentes tailles de quadrats (ensemble de pixels) centrés sur un pixel occupé ont été considérées comme étant les habitats disponibles à plus fine échelle.

Les précocités de blé présentent une structure spatiale fine (portée de l'autocorrélation : 1200 m mais forte autocorrélation jusqu'à 600m seulement). Des zones sont donc plus précoces que d'autres. En outre, malgré des variations annuelles des précocités moyennes observées sur l'ensemble de la zone d'étude (figure B.6), cette structure semble être conservée d'une année sur l'autre (voir la carte moyenne dans la section en anglais). Elle dépend en partie de facteurs abiotiques tels que les températures et les caractéristiques du type de sol. Cependant, la faible portée de l'autocorrélation spatiale suggère que d'autres facteurs tels que les pratiques agricoles conduites par les différents agriculteurs sur leurs parcelles (sous l'hypothèse que ces parcelles sont agrégées dans l'espace) pourraient intervenir.

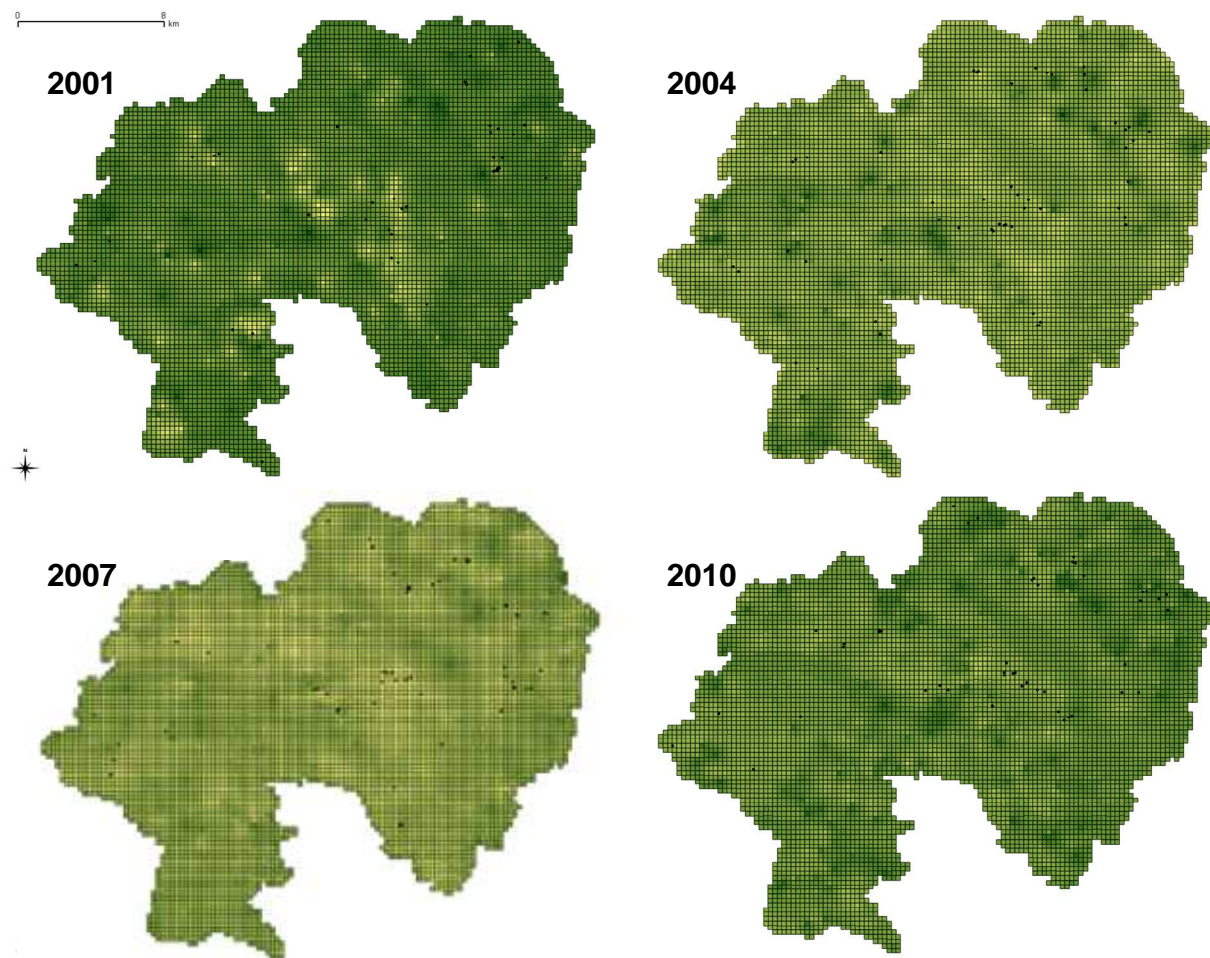


Figure B.6 : Distribution spatiale des précocités de blé (gradient du jaune : blé précoce au vert : blé tardif) et des nids de Busard cendré (points noirs) pour 4 années de la période d'étude





La localisation des nids de Busards cendrés dans le blé est influencée par la distribution spatiale des précocités de blés à l'échelle de la zone d'étude: les individus tendent à s'agréger dans les zones où le blé est globalement plus précoce (figure B.6). La localisation de ces zones précoces est relativement stable d'une année sur l'autre et l'autocorrélation spatiale des précocités de blé jusqu'à 1200 m est proche de la taille d'une colonie, ce qui suggère que ces zones précoces pourraient correspondre à la position des colonies et expliquer la relative stabilité de leurs localisations d'une année à l'autre. Cependant, certaines zones de blés précoces ne sont pas toujours choisies par le Busard cendré car d'autres facteurs tels que l'abondance des proies (campagnols des champs) et l'évitement des bois et villages interviennent dans la sélection d'une zone (de Cornulier 2005, Cornulier and Bretagnolle 2006). A fine échelle (de 250 à 1000 m autour du nid), la précocité des blés du pixel choisi par un couple diffère peu de celle des pixels voisins. En revanche, les individus les plus précoces, en termes de date de ponte, tendent malgré tout à choisir les pixels où le blé est plus précoce parmi ceux disponibles dans un rayon de 1000m.

Ces résultats appuient ceux obtenus dans le chapitre précédent : les individus précoces sont capables de distinguer la qualité relative des patchs à plusieurs échelles spatiales et choisissent les patchs où le blé est plus précoce tandis que les individus plus tardifs choisissent des patchs de blé plus précoces à large échelle mais pas localement. Par définition, les individus tardifs (de moins bonne qualité) se reproduisent plus tard quand la précocité relative des blés n'est plus un proxy de leur hauteur et donc de leur qualité. Cependant, la structure des précocités de blés (autocorrélation spatiale des précocités jusqu'à 1200m : les pixels considérés aux fines échelles ont des précocités de blé proches) et le pattern de sélection obtenu suggère que, par attraction conspécifique, ces individus auraient tendance à s'installer à proximité des individus précoces (*article 3*) et présentent ainsi une sélection à large échelle. En revanche à plus fine échelle, une certaine compétition entre les couples pourrait contraindre les individus tardifs à nicher à une certaine distance de leurs congénères précoces (dans un autre pixel) d'où l'absence de sélection à cette échelle.

La sélection de l'habitat physique de reproduction du Busard cendré est un processus s'effectuant à plusieurs échelles spatio-temporelles. Cette étude souligne l'importance de considérer différentes échelles spatiales dans l'étude de la sélection d'habitat. Notre approche multi-échelle révèle en effet des patrons de sélection et des processus différents selon l'échelle considérée. Elle attire l'attention sur l'importance de considérer l'aspect social dans

la sélection d'un site de nidification chez une espèce coloniale ou semi-coloniale comme le Busard cendré.

Les facteurs influençant fortement et négativement la fitness des individus sont le plus souvent évités à large échelle spatio-temporelle (Rettie and Messier 2000). Dans notre étude, ce sont les zones de blé à phénologie tardive qui sont globalement évitées, la conservation du Busard cendré devrait donc davantage se concentrer sur les zones à blés précoces afin de maximiser la fitness des individus.

Dans le contexte du changement global, nous n'avons pas mis en évidence d'avancée des phénologies de blé sur 10 ans d'étude. Cette période est cependant relativement courte et des interactions entre changement climatique et changement d'usage des sols effacent vraisemblablement toute tendance. Nous avons toutefois dégagé des variations temporelles de phénologie non négligeables qui annuellement influencent la sélection (*article 2*) et qui, à plus long terme, pourraient présenter une tendance à l'avancée et ainsi potentiellement favoriser la colonisation de nouvelles zones par le Busard cendré.



## ***B.IV.2. Article 4***

### **Breeding habitat selection of a farmland ground-nesting bird: an approach at multiple spatio-temporal scales using remote sensing**

Gillis H.<sup>1\*</sup>, Le Rest K.<sup>1</sup>, Guérif M.<sup>2</sup>, Castillo S.<sup>2</sup>, Weiss M.<sup>2</sup> and Bretagnolle V.<sup>1</sup>

<sup>1</sup>CNRS-UPR 1934, Centre d'Etudes Biologiques de Chizé, 79360, Beauvoir sur Niort, France

<sup>2</sup>INRA- UMR 1114, Domaine Saint Paul ; Site Agroparc ; 84914 Avignon Cédex 9

\*Corresponding author : Hanneke Gillis

E mail: [gillis@cebc.cnrs.fr](mailto:gillis@cebc.cnrs.fr); [hanneke.gillis@yahoo.fr](mailto:hanneke.gillis@yahoo.fr)

Article en préparation



### ***Abstract***

Habitat selection is a crucial process by which an animal chooses which resources and conditions to use in order to maximize its survival and breeding success. Interpretations of habitat selection patterns and processes are highly dependant on the chosen scales. By using an approach at multiple spatio-temporal scales, we investigated breeding habitat selection of Montagu's harrier *Circus pygargus*, which is a semi-colonial ground-nesting raptor mostly breeding in tall wheat crops. We first explored spatio-temporal structure of a proxy of habitat quality (i.e. wheat precocity), provided by remote sensing technology, and then compared it with nest densities and positions over 10 years. We found that wheat precocity was spatially structured and that this spatial structure was overall the same between years. Abiotic factors, i.e. temperature and pedology were partly responsible of this structure but the small autocorrelation range suggested that farmers' practices may also play a key role in observed patterns. This spatial structure overall influences Montagu's harrier nest positions in farmland landscapes. Both early and late breeders seem to nest in areas with precocious wheat at the broader scale (i.e. 460 km<sup>2</sup>). However, we found differences in the strength of selection in favour of high habitat quality at small spatial scale according to individual laying date. Only early breeders tended to select precocious wheats at this scale (i.e. 1 km around nests). Pattern found at broad scale may highlight a conspecific attraction of late breeders (low-quality) in areas chosen by early (and high-quality) breeders while pattern found at finer scales may underline some competition between individuals preventing late breeders to nest in the same patch than early ones. We thus detected different patterns and mechanisms of habitat selection depending on the spatio-temporal scale considered.



## ***Introduction***

Habitat selection is commonly viewed as a process which operates at multiple spatial and temporal scales (Johnson 1980, Hutto 1985, Orians and Wittenberger 1991, Hall et al. 1997). Through this process, an animal chooses which resources and conditions to use to maximize survival or breeding success (Hall et al. 1997). Breeding habitat selection plays a key role in the fitness of individuals. Therefore, individuals are under strong selective pressures to perform optimal breeding habitat choice (Doligez et al. 2003). However, some individuals often failed in their breeding attempt, which underlines the complexity of habitat selection process. At individual point of view, the choice to install or not in a patch may be based on integrative information about patch quality at particular spatial and temporal scales.

The definition of the spatial and temporal scales is thus a crucial issue to underline the process under study (Johnson 1980, Wiens 1989, Saab 1999, Rettie and Messier 2000). Studying individual decisions at relatively broad spatial and temporal scales should have the potential to reveal habitat features more important to fitness than those made at finer scales (Rettie and Messier 2000). Broad scales are indeed more likely to provide generalizations than fine scales (Wiens 1989). However, interpretations of ecological patterns and processes at one scale may not apply at other scales (Wiens 1989). Some authors suggest that performing spatial multi-scale analyses is capital in habitat selection studies (Orrians and Wittenberger 1991). However, studies using this kind of approach for habitat selection are still scarce (Martínez et al. 2003). For temporal scale, it is essential to consider the temporal heterogeneity by acquiring long-term data (Wiens 1977, Block and Brennan 1993), especially in habitat selection studies. This permits to understand the influences of highly fluctuating and complex processes but also to avoid misleading interpretation with short-term studies.

Scale choices further depend on the studied species (Wiens 1989, Allen and Hoekstra 1993, Forman 1995, Saab 1999) and so do habitat features choice. Here, we wanted to study breeding habitat selection in a long-living and migratory ground-nesting bird, the Montagu's Harrier *Circus pygargus*. The species breeds in loose colonies (relatively fixed in space, year to year, Arroyo et al. 2002, Arroyo et al. 2004), mainly in wheat crops in Western Europe (Cramp and Simmons 1980) and nest location highly depends on vegetation height (Limiñana et al. 2006, Limiñana et al. 2011, Gillis et al. [b] in review). We expected that nest choice may therefore operate at multiple spatial and temporal scales. First, year to year, early individuals arriving on their breeding sites may choice in which (future) colony they will install according



to breeding success in previous years and/or relative macro-patch quality. Second, once the first choice made, individuals may select at a finer scale (i.e. intra-colony and seasonal scales) in which micro-patch to nest according to conspecifics presence and micro-patch quality. We therefore had to account for species strategy to define scales.

The choice of spatial and temporal scales is sometimes defined according to the process under study, but more often it is constraint by human perceptual abilities, technological or logistical limits (Levin 1992). Acquiring habitat data at relatively broad spatial and temporal scales is not evident. However, the emergence of the use of remote sensing in the 1980s has considerably facilitated habitat data collection at broad spatial and temporal scales. This method could provide information about plant species, plant productivity, and vegetation dynamics, i.e. phenology (Myneni et al. 1997, Zhang et al. 2003). The trade-off between observation frequency, geographical coverage and spatial resolution has for long hampered the use of remote sensing for characterizing vegetation at more local scales. The availability of medium spatial resolution sensors (250 m) like Modis offers new possibilities of vegetation monitoring (Boschetti et al. 2009, Jenerette et al. 2010, Sakamoto et al. 2010, Hwang et al. 2011) with an historical depth of a decade.

Our objectives were thus multiple. We first used remote sensing data over ten years to determine the spatial structure of a proxy of habitat vegetation height and thus quality (i.e. wheat precocity). Then, we linked this spatio-temporal structure of patch quality to nest positions of Montagu's harrier, accounting for external information about spatial distribution of soils and climate over the region. Both macro and micro-patch selections were investigated: macro-patch refers to the entire study area (i.e. about 500 km<sup>2</sup>) while micro-patch refers to small quadrats centred on each nest (between 0.5 km<sup>2</sup> and 5 km<sup>2</sup>).

## ***Materials and methods***

### **Study area and species**

This study was carried out in an intensively managed farming landscape located in central-western France (Deux-Sèvres: 46°11'N, 0°28'W). Since 1994 and every year, land use has been monitored for each field (about 19,000 fields in total). This area covers nearly 500 km<sup>2</sup>, and crops are dominated by wheat (45% of total area), colza (9%) and spring-sown crops (24%, i.e. maize, sunflower). Hedges are greatly reduced and fragmented and are confined to the vicinity of villages and farms. Some woodlands still remain but in modest sizes (3% of the



total area). This area faced high agriculture intensification that has resulted in an increase in field size (in 2010, mean  $\pm$  standard error:  $3 \pm 0.003$  ha). Crops are characterised by highly homogeneous within-field vegetation structure (height, density and species composition). However, there is a wide between-field variability in vegetation dynamics both between and within crop types, as a consequence of differences in agricultural practices in addition to soil characteristics.

On this study area, the Montagu's harrier, which is a migratory raptor, arrived in early April for breeding. In this species, observed nest aggregation is partly explained by landscape structure (i.e. avoidance of built-up areas and woodlands, de Cornulier 2005, Cornulier and Bretagnolle 2006) but also by benefits provided by coloniality (i.e. cooperative defence against predators, Arroyo et al. 2001). In French farmland particularly, breeding density and breeding success of this raptor are also strongly affected by the abundance of its main prey, the common vole *Microtus arvalis* (Millon et al. 2002). From 2001 to 2010, nests were systematically searched through an intensive searching effort. Note that it is relatively easy to locate them by observing the adults during the pre-laying (aerial displays by males), incubating and chick rearing stages (food provisioning by the male; Cornulier and Bretagnolle 2006). Nest geographical coordinates were precisely noted. Additionally, nests were monitored to collect data on breeding parameters in particular the date of laying. Laying date was directly estimated from nest visit during laying or indirectly estimated by back-calculated from chick and/or egg measurements (see the methodology used by Millon et al. 2002). 603 nests were found over the study period (from 33 to 79 nests/year). Among them, 470 were located in wheat (78%, from 27 to 60 nests per year). Over the study period, average laying date ( $\pm$  SD) of Montagu's harriers nesting in wheat fields was May 11<sup>th</sup> ( $\pm$  16 days) with some among-year variations (minimal: May 7<sup>th</sup>  $\pm$  20 days and maximal: May 22<sup>nd</sup>  $\pm$  14 days in 2003 and 2009 respectively). Salamolard et al. (2000) demonstrated that annual variations in number of nests and laying dates were partly due to variations of the abundance of common voles.

#### Remote sensing habitat and environmental data

From Modis data, we were interested in obtaining a spatio-temporal description across our study area of two characteristics: (i) crops canopy growth, that is attainable from surface reflectance data and adequate inversion algorithms, and (ii) the climatic variability expressed through surface temperature.



We acquired, from 2001 to 2010, daily Modis surface reflectance at 250m and 500/1000 m resolution (MOD09GQ and MOD09GA) and the daily surface temperature at 1000 m resolution (MOD11A1) over our region of interest from the Land Processes Active Archive Center website (<https://lpdaac.usgs.gov/lpdaac/>).

#### *Wheat Leaf Area Index and wheat precocity index from surface reflectance data*

Using the quality information contained in the MOD09GA product, we excluded in the MOD09GQ product the pixels concerned by cloud contamination as well as the pixels with a view zenith angle higher than 65° (NAN values for red and infrared reflectance values). The map was converted from Sinusoidal projection to French Conical Lambert II étendu projection thanks to the Modis Reprojection Tool (same website as above). The series of images were superimposed to the land use map provided yearly by ground surveys, and an area-ratio of 85% (i.e. at minimum 85% of a 250 m pixel's area had to be occupied by wheat) was applied to select Modis pixels across the region. For each selected pixel, NDVI values were calculated and the yearly NDVI time evolution profiles were smoothed (thanks to an algorithm limiting the variation range over a five date interval); the objective was to eliminate the non-coherent values – and corresponding dates - due to remaining atmospherical and directional effects. Leaf Area Index (LAI) values were therefore calculated from the red and near infrared reflectance values thanks to the algorithm proposed by Baret et al. 2007, based on neural networks trained on radiative transfer models into the canopy.

The yearly time evolution profile (Fig. 1) was therefore described by a logistic-exponential function of the cumulated growing degree-days for each pixel (Lauvernet 2005):

$$LAI_t = LAI_x \left( \frac{1}{\left(1 + \exp^{-A(GDD_t - T_0 - T_i)}\right)^c} - \exp^{-B(GDD_t - T_0 - (T_i + dTS))} \right) \quad \text{Eq.1}$$

With :

$LAI_t$ , the leaf area index of the crop at date  $t$  ,

$t$ , the cumulated days from 1<sup>st</sup> of October of the year previous wheat harvest,

$GDD_t$ , the cumulated growing degree-days (with a base of 0°C) from the origin up to date  $t$ ,

and the parameters:

$LAI_x$ , the asymptotic maximum value of  $LAI$ ,  $T_0$  the  $GDD$  value at wheat emergence,

$T_i$ , the  $GDD$  value at the inflexion point of the growing part of  $LAI$ ,

$dTS$ , the differential  $GDD$  value between  $T_i$  and the time when senescence is completed,

$A$ , the  $LAI$  growth rate at inflexion point.  $B$  the  $LAI$  growth rate at senescence

$c$ , representing the more or less symmetrical aspect of the growing part.



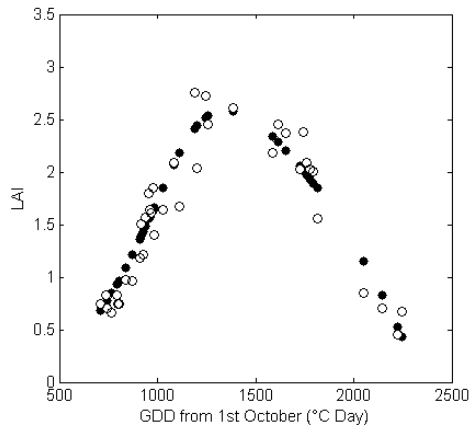


Fig.1: LAI time evolution for a Modis wheat pixel: (o) estimated LAI from red and near infrared surface reflectance; (●) adjusted LAI through Eq. 1.

A was calculated from the constraint of having  $LAI=0$  at  $T_0$ . The parameters were estimated through a Bayesian method of Importance Sampling (Guérif et al. 2006) allowing proposing an adjusted LAI time evolution profile for each wheat pixel (Fig. 1) and mapping yearly parameters values across the region. Among those parameters, we were particularly interested in the  $T_i$  parameter which expresses the precocity of wheat growth in spring (Fig. 2). This  $T_i$ , expressed in degree-days was back-transformed in julian days (from January 1<sup>st</sup>) and was used as a proxy of habitat quality.

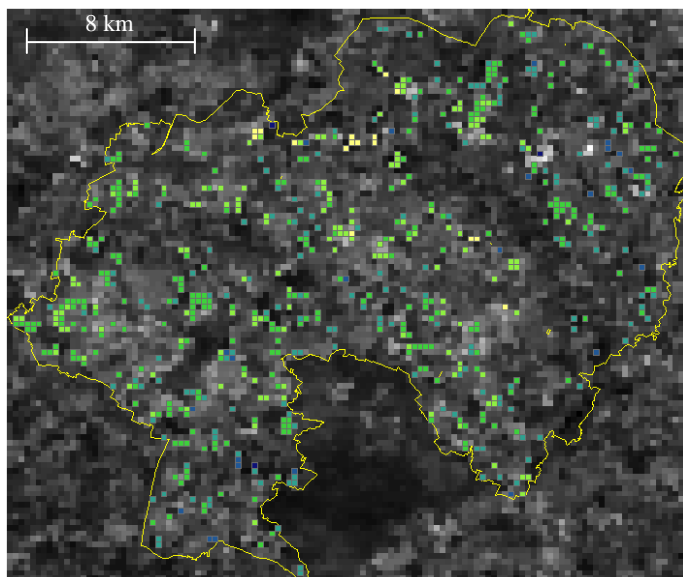


Fig. 2: Map of  $T_i$  values (translated in calendar dates) for year 2006

The Modis Land Surface Temperature product (MOD11A1) was projected like the reflectance data into Lambert II étendu and resized to a 250 meters resolution; we used their included quality control information to select only pixels having a good data quality, i.e. free from cloud contamination, and acquired on the same orbit. Sums of surface temperature were calculated for each pixel by summing all the daily values over 3 months periods (January to March) in order to provide maps (Fig. 3).

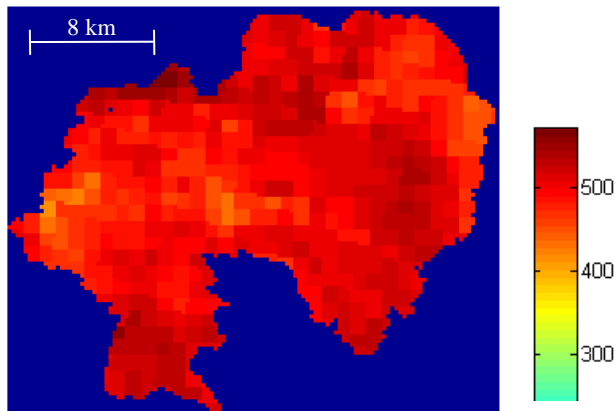


Fig. 3: Sums of surface temperature from January 1<sup>st</sup> to March 31<sup>st</sup> in 2003.

### Analysis

#### *Spatio-temporal structure of wheat precocity over the entire study area*

Habitat data provided by remote sensing consisted in a spatio-temporal partial grid (pixel size: 250 × 250m) where estimations of wheat precocity were only available for some locations and some years. As detailed in previous section, wheat precocity estimations only concerned pixels covered by at least 85% of wheat. However, Montagu's Harriers were prone to nest in all available wheat fields. Interpolation, using a geostatistical methodology, was therefore required in order to estimate wheat precocity of each pixel. We chose the method of Kriging with External Drift (KED, Hengl et al. 2003) since it allows using external information improving the estimates through a linear model with spatially structured residuals. We included year, surface temperature (provided by remote sensing, positively related with wheat growth and therefore precocity) and two variables of pedology (source: Poitou-Charentes IGCS Program run by the Regional Chamber of Agriculture, the IAAT and INRA): five soil categories and the available water content of soil (that may exert limitation on wheat growth, i.e. winter waterlogging for some soils in humid conditions, water stress for others in particularly dry years,...). The wheat precocity model (Eq.2) used for KED was the following spatio-temporal model:

$$E[T_i] = \mu + SurfTemp + Year + SWC + Pedo + SurfTemp \times Year \quad \text{Eq.2}$$

$T_i$ , wheat precocity index ( $E[\ ]$  is the Esperance, i.e. the predicted mean)

$\mu$ , a constant parameter also known as "Intercept"

$SurfTemp$ , the land Surface Temperature

$Year$ , a 10 level-factor (from 2001 to 2010)

$SWC$ , the soil water content

$Pedo$ , soil type (a 6 level-factor)



Kriging was performed for each year between 2001 and 2010 by considering the previous spatio-temporal linear model and by adjusting an exponential family variogram on model residuals accounting for spatial structure in wheat precocity. Interpolated grids were then used to explain nest positions at two different spatial scales: the macro-patch scale representing the entire study area and the micro-patch scale representing local nest position. For micro-patch scale selection, we defined quadrats centred on each nest. We tested several different quadrat sizes: from 0.5 km<sup>2</sup> to 5 km<sup>2</sup>.

#### *Nest position at macro-patch scale*

Here, we investigated the effect of wheat precocity on harrier nests position at macro-patch scale (i.e. the scale of the entire study area). Nests position at macro-patch scale was a point process determined by many covariates and presenting, in our case, spatial and temporal dimensions (Diggle and Gabriel 2010). Point processes could be analysed by several methods (see Gatrell et al. 1996 for a description of the main point process analyses). We used the most popular point process model: the Poisson model, which is useful to explore covariate influences (Lawless 1987). Therefore, a count data (i.e. number of points per unit of surface) was constructed by extracting the number of nests per pixel of the wheat precocity grid. A generalized linear model was then built to test the effect of wheat precocity on nest density. The proportion of wheat in each pixel was used as an offset in order to correct linearly the number of nest in wheat in each pixel by its amount of wheat. These count data presented a spatio-temporal structure and a high number of zero values (i.e. pixel without any nest). Because of their proximity, pixels may not be spatially and temporally independent of each others. We thus checked the existence of spatial and/or temporal autocorrelation in the model residuals. On the other hand the high proportion of zero (about 99%) also called Zero-Inflated count data was a form of overdispersion. Both spatio-temporal autocorrelation and overdispersion lead to underestimation of the standard error of model parameters i.e. biased statistical tests (Haining et al. 2009). To avoid misleading interpretations, we used a bootstrap methodology to estimate an unbiased standard error for wheat precocity parameter by generating subsets of data including only residually independent kriging estimations in space and time. Variograms built from spatial and temporal scales were thus examined in order to guaranty independence of residuals. We chose a threshold distance equal to the range of variograms and generate randomly subsets respecting this threshold between all kriging



estimations. A Zero-Inflated Poisson model (ZIP, Lambert 1992) was also preferred to a Poisson model to account for the high proportion of zero. It consisted in a mixture distribution between a probability of nest presence (including only a constant parameter, see Eq. 3) and a Poisson distribution, i.e. number of nest (including a constant parameter, an offset and our regression coefficient of interest for the wheat precocity, see Eq. 4). The expected number of nests (see Eq. 5) was then the multiplication between the probability of presence and the number of nests from the Poisson distribution. Thus, if probability of presence is low (near zero), the model tends to predict a higher occurrence of zero than expected by a simple Poisson distribution. 10 000 bootstraps were generated and the parameter estimate for the wheat precocity was each time stored in order to examine the full parameter distribution. we could then calculate an unbiased confidence interval for the parameter of interest. The following Zero-Inflated Poisson ZIP model was thus considered:

$$\text{logit}[E[\text{Zero\_nest}]] = \mu_1 \quad \text{Eq. 3}$$

$$\ln(E[\text{Count\_nest}]) = \mu_2 + \%Wheat + \beta T_i \quad \text{Eq. 4}$$

$$E[\text{Nb\_nest}] = E[\text{Zero\_nest}] * E[\text{Count\_nest}] \quad \text{Eq. 5}$$

$E[]$ , Esperance, i.e. the predicted mean

$\text{Zero\_nest}$ , Probability of presence of nest per pixel from the first part of the ZIP model (Binomial distribution)

$\mu_1$ , Constant parameter for the first part of the ZIP model

$\text{Count\_nest}$ , Number of nest per pixel from the second part of the ZIP model (Poisson distribution)

$\mu_2$ , Constant parameter for the second part of the ZIP model

$\%Wheat$ , Offset for the second part of the ZIP model (percentage of wheat in the pixel)

$T_i$ , Wheat precocity index

$\beta$ , Parameter of interest (associated with the wheat precocity index)

$\text{Nb\_nest}$ , Number of nest per pixel from the full ZIP model

### *Nest position at micro-patch scale*

Micro-patch was realized on four quadrat classes differing in size: 0.5625 km<sup>2</sup>, 1.5625 km<sup>2</sup>, 3.0625 km<sup>2</sup>, and 5.0625 km<sup>2</sup> (fig. 4). The first quadrat class included a central pixel and the pixels directly adjacent to it (i.e. first ring of pixels around the target one, leading to a total of 9 pixels). On the same principle, the second quadrat class included an additional ring of neighboring pixels (25 pixels) and so on for the three larger quadrat classes. Nest was always located in the centre of the quadrat, which lead to a symmetric spatial configuration.

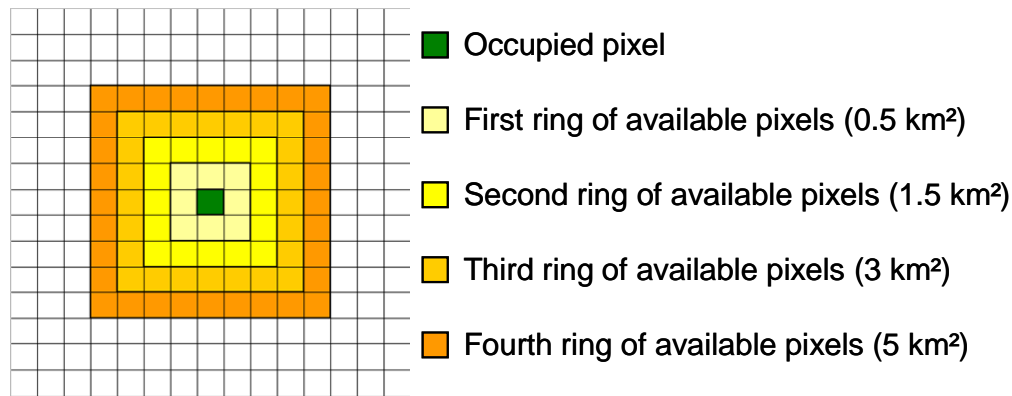


Fig. 4: Design of quadrats used for fine scale analyses. One square represents a pixel of 250m of the Modis grid. For each quadrat size, previous ring(s) of pixels were included in the available pool of pixels

An index reflecting the selected wheat precocity for nesting relatively to wheat precocity of neighboring pixels was calculated. It was the mean of differences between precocity of each neighboring pixel and the wheat precocity of the central pixel. When this index was positive, the nest was located at a precocious place relatively to the local available precocity of wheat. When null, the nest was positioned at the mean of wheat precocity in the micro-patch (i.e. random selection). Finally, when negative, the nest was positioned at a tardy place relatively to neighbour. The effect of the laying date on the wheat precocity selected for nesting was further investigated as we expected that early breeders were more constrained to build their nests in precocious wheat (i.e. higher wheat height in early season; Gillis et al. [b] in review). A linear model (Eq. 6) was therefore performed between the index of relative precocious of wheat and the laying date for each of the four micro-patch scales.

$$E[\text{MeanDiff}] = \lambda + \delta * \text{Laying\_date} \quad \text{Eq. 6}$$

$E[\ ]$ , the Esperance, i.e. the predicted mean

*MeanDiff*, Mean of differences between the precocity at neighbours pixels and at the selected pixel

$\lambda$ , Constant parameter indicating the mean of MeanDiff

$\delta$ , Regression coefficient associated with the laying date.

## Results

### Spatio-temporal structure of wheat precocity over the entire study area

The visual range of the variogram performed on wheat precocity data, by including environmental information, was about 1.2 kilometers (Fig. 5), which is relatively small



compared to the range of the study area (20 km). The sill was about 200 units and there was no nugget. This variogram revealed a strong spatial autocorrelation of wheat precocity between 0 and 0.6 km before attenuation up to 1.2 km, the distance beyond which the autocorrelation is no longer detectable (Fig. 5).

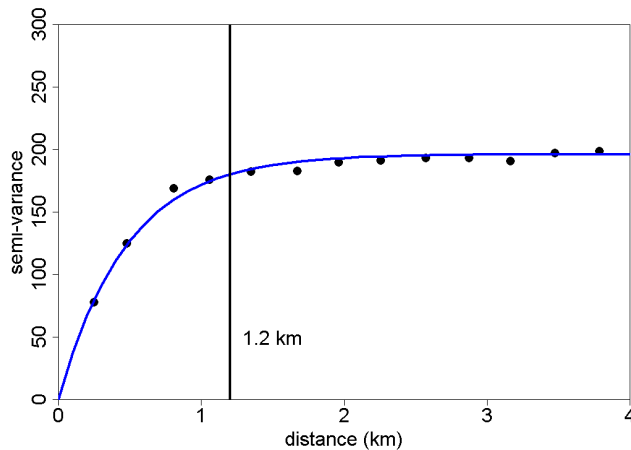


Fig. 5: Variogram on residuals of the wheat precocity model. Black dots represented the empirical variogram while the blue line is the adjusted variogram. Vertical line indicated the range of the spatial autocorrelation

We did not detect any temporal trend in mean wheat precocity over the study period (Fig. 6). However there were strong variations between years, which confirm the need to incorporate year in the model.

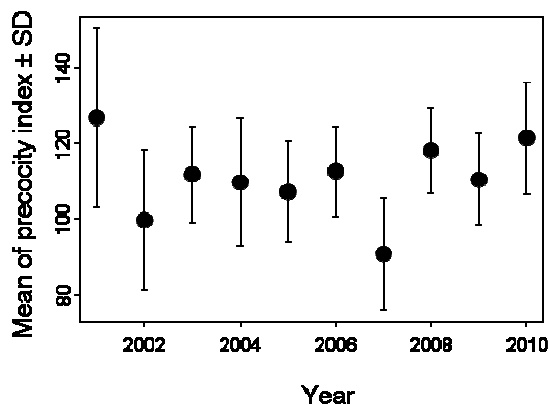


Fig. 6: Temporal variation of wheat precocity (in julian days) between 2001 and 2010

KED was performed on the entire grid of the study area for each year of the study period but only the mean over 10 years is presented in Fig. 7. Wheat precocity appeared to be highly structured in space and the mean wheat precocity estimation map pointed out precocious places *versus* late places and their constant locations in space through years (Fig. 7). Indeed, if high among-year variations in wheat precocity spatial structure had occurred, such general pattern should not have been found (i.e. a more uniform mean map should be found). Wheat precocity ranged from 92 to 134 julian days, indicating important differences of wheat precocity over the study area. Interest of this map was to superpose Montagu's harrier nests

(only those located in wheat) and determine if nests were randomly distributed or not through the wheat precocity gradient.

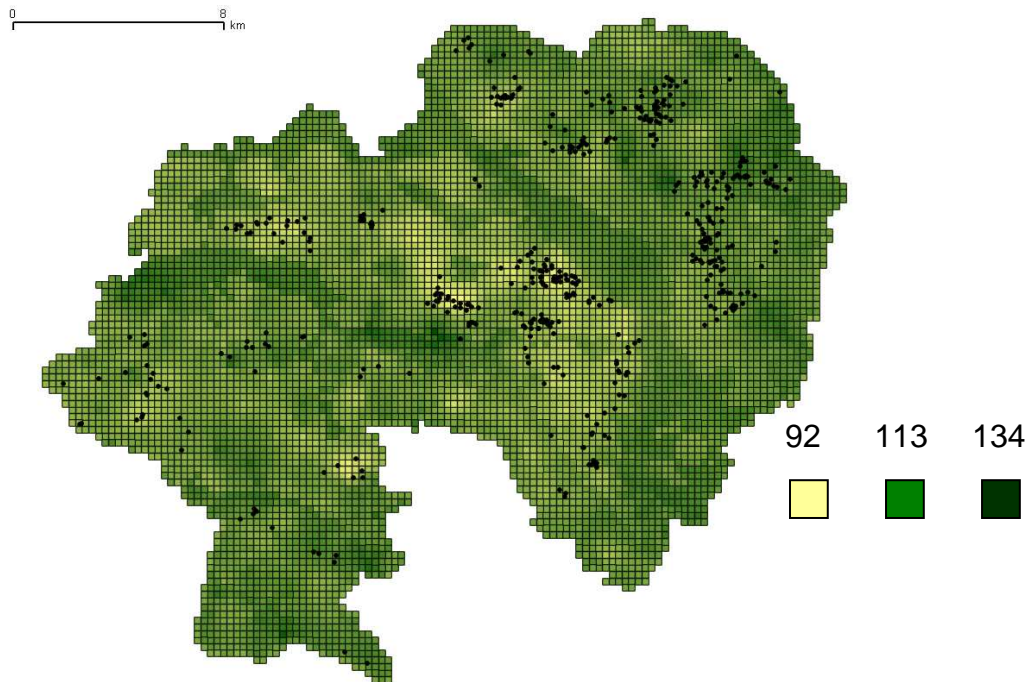


Fig.7: Mean of the predicted wheat precocity between 2001 and 2010 (in Julian days) and position of nests during this period (black dots). Here we considered that all the area was covered with wheat.

### Nest position at macro-patch scale

Parameter estimate of the ZIP model associated with wheat precocity ( $\beta$ ) indicated there was a strong negative influence of late wheat (high  $T_i$ ) on the number of nests (Tab. 1).

Tab. 1: Parameter estimates of the Zero Inflated Poisson model

Parameter	Estimate	Std. Error	p-value
$\mu_1$	- 2.05	0.18	<2e-16 ***
$\mu_2$	- 1.72	0.16	< 2e-16 ***
$\beta$	- 0.26	0.05	1.42e-08 ***

However the associated standard error (and thus the p-value) might be incorrect if there was autocorrelation in residuals. Spatial and temporal autocorrelation on the ZIP model residuals were therefore checked (Fig. 8). We found a positive spatial autocorrelation for distance less than 750 meters between pixels (Fig. 8a) but no temporal autocorrelation (Fig. 8b). Standard errors and p-values from the ZIP model were therefore underestimated.

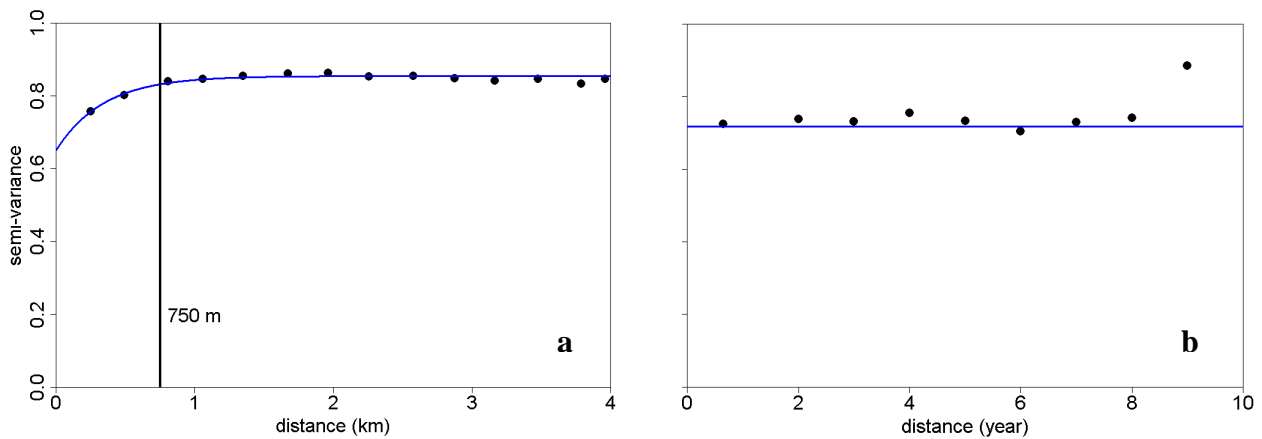


Fig. 8: Variograms on the ZIP model residuals in space (a) and time (b). Black dots represented the empirical variogram while the blue line is the adjusted variogram. Vertical line indicated the range of the spatial autocorrelation

To avoid this problem, a bootstrap process was implemented to correct the standard error estimates by selecting successive subsets of data with pixels with a minimum distance of 750 m between each other. 10000 random subsets were generated respecting this threshold distance and the parameter of wheat precocity was each time estimated.

Bootstrap provided a new estimate of wheat precocity parameter ( $\beta = -0.26 \pm 0.19$ ) but it was insignificant according to a threshold  $\alpha = 0.05$  (Fig. 9). However the global distribution of  $\beta$  tended to be negative (93% of the 10000 estimations of  $\beta$  are negatives, Fig. 9), which indicate that the number of nests seemed to be more important in precocious pixels but not significant at macro-patch scale.



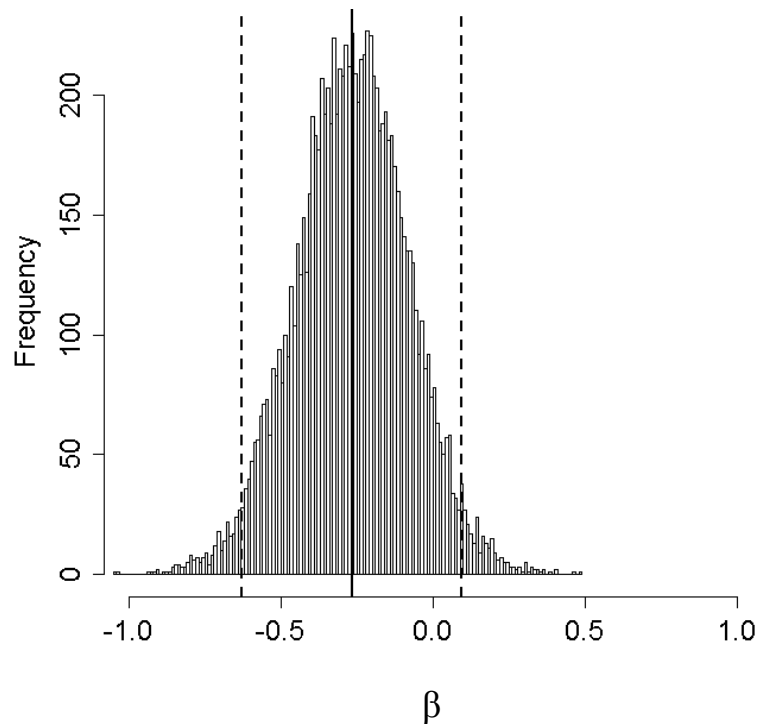


Fig. 9: Wheat precocity parameter estimates ( $\beta$ ) from the 10000 bootstraps: dotted lines are the 95% confidence interval and solid line is the median.

#### Nest position at micro-patch scale

The effect of wheat precocity on nest position was further investigated at micro-scales by considering five nest centered quadrats of different sizes (0.5 to 5 km<sup>2</sup>) and by calculating the mean difference of wheat precocity between the neighbour pixels and the selected pixel (i.e. occupied pixel) labelled “MeanDiff”.

Distributions of “MeanDiff” index suggested that selected pixel for nesting was not more precocious than pixels at neighbour (Fig. 10). This was particularly true at very fine scales (Fig. 10a and 10b) where median was about zero. However, at some larger scales (Fig. 10c and 10d) median became positive indicating a trend of selection in favour of precocious pixels for nesting.

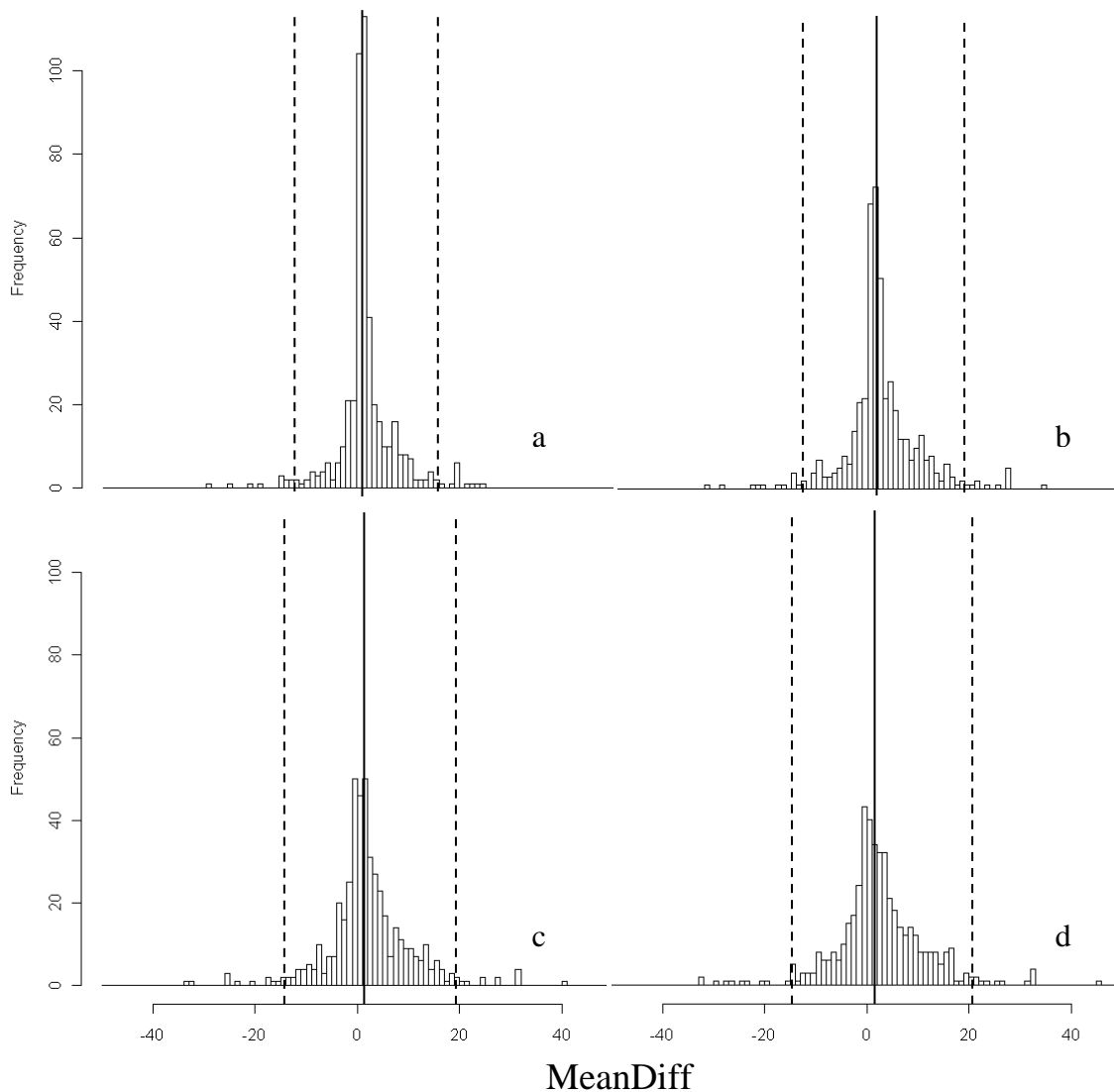


Fig. 10: Micro-patch selection of wheat precocity considering four classes of quadrats: 0.56 km<sup>2</sup>(a), 1.56 km<sup>2</sup> (b), 3.06 km<sup>2</sup> (c), 5.06 km<sup>2</sup>(d). Positive values on the X axis indicate that the selected pixel was more precocious than others. Dotted lines are the 95% confidence interval and solid lines are medians of the distribution.

There were high variations in wheat precocity selection (from -40 days to +40 days), underlining the lack of important covariates in the model. Therefore, the effect of laying date was investigated supposing that earlier pairs are more constrained to choose a precocious place than others (Tab. 2). A positive selection for precocious wheat was found whatever the quadrat considered (Tab. 2). This relative habitat selection is stronger for larger quadrats. Laying date have a negative effect on this selection whatever the quadrat considered. However this effect was only significant for the larger quadrat. Thus, early breeders tended to select precocious wheat for quadrats of 5.06 km<sup>2</sup>.

Tab. 2: Parameter estimates from the linear model of micro-patch selection applying at the four quadrats classes.  $\lambda$  is the global selection of wheat precocity and  $\delta$  is the laying date effect.

Quadrat	Parameter	Estimate	Std. Error	p-value
0.56 km <sup>2</sup>	$\lambda$	1.62	0.71	0.02 *
	$\delta$	-0.02	0.02	0.26
1.56 km <sup>2</sup>	$\lambda$	2.78	0.89	2e-03 **
	$\delta$	-0.03	0.02	0.13
3.06 km <sup>2</sup>	$\lambda$	3.82	1.02	2e-04 ***
	$\delta$	-0.04	0.02	0.07
5.06 km <sup>2</sup>	$\lambda$	4.51	1.09	4e-05 ***
	$\delta$	-0.05	0.02	0.047 *

### Discussion

In this study, we demonstrated that habitat quality (i.e. wheat precocity) exhibited a spatial structure at a fine scale and that this structure seems to be relatively stable one year to the other. This spatial structure overall influences Montagu's harrier nest positions in farmland landscapes. Indeed, breeders seem to nest in areas with precocious wheats at a macro-patch scale (i.e. study area scale). However, our multi-scale approach highlights differences in the strength of selection in favour of high habitat quality, at local spatial scales, according to individual date of laying. Indeed selection of precocious wheat ( $\lambda$ ) and laying date effect ( $\delta$ ) were stronger at 5 km<sup>2</sup> than at other quadrat sizes.

The observed spatial structure of habitat quality is partially due to the abiotic factors we took into account, i.e. temperature and soil characteristics. However, these abiotic factors could not explain the small spatial autocorrelation range (i.e. 1,2 km) suggesting that other factors are acting at smaller scale. Since wheat growth is highly depend on agricultural practices (i.e. sowing date, wheat variety and fertilization), some of the observed structure may be due to differences in practices conducted by each farmer on his land. We did not detect any trend in wheat phenology over the study period, neither in its annual mean nor in its spatial structure. This pattern suggests that farmers' practices may not have evolved over 10 years and that climate did not change or that the interaction between these two components of global change lead to the absence of trend.

At macro-patch scale (i.e. study area scale), nest densities tended to be higher where wheat is precocious. However, taking into account spatial autocorrelation of model residuals led to insignificant relationship between nest densities and wheat precocity. These findings may come from methods used: i) interpolation method estimated mean values of wheat precocity where distance between observations and non-sampled points was higher than the



spatial autocorrelation range of wheat precocity, which generate noise in kriging estimations and ii) bootstrap generated less powerful subsets (about 1/10 of the initial dataset) by deleting nearest kriging estimations (considered as exact repetitions) but they are actually only pseudo-repetitions. Therefore, our methodology tended to overestimate the true confidence interval for the parameter of interest  $\beta$  and a more parsimonious methodology may be used. Moreover, the distribution of wheat precocity coefficient estimates highly suggests that harriers densities were higher in precocious wheat areas. Given that wheat precocity is spatially structured and nest densities depend on wheat precocity, nests presented, by deduction, a spatial structure and aggregated in area where wheat is early (i.e. colonies). Since this spatial structure is constant over years, nest positions and thus colonies are also stable through years. These findings support the hypotheses that stability in colony positions are expected under habitat stability (Burger 1982), here wheat phenology stability and that colony formation, at least in this species, may be partly due to the spatial structure of favourable habitats (Danchin and Wagner 1997). Wheat precocity and nests positions are thus predictable at large scale even if the agricultural system is highly disturbed (in contrast to Levin 1992 expectations). Some precocious wheat areas were however not occupied by harriers. These unoccupied areas may be located next to villages and woodlands, which are known to be avoided by harriers (Cornulier and Bretagnolle 2006). Additionally, food abundance and distribution may play a role in nest positions (de Cornulier 2005). At the study area spatial scale, one step further will be to consider spatial and temporal variations in food abundance and presence of village and woodlands to improve habitat quality estimations.

At finer scale (micro-patch scale), we detected a slight selection whatever the scale chosen (from 0.5 to 5 km<sup>2</sup> quadrats). This selection had not the same intensity according to the size of the quadrat considered. This may be partly due to the small spatial autocorrelation range of wheat quality: as a consequence, wheat precocities of available pixels around nests and select ones were relatively homogenous for small quadrats. We also found that selection at these spatial scales was modulated by individual laying dates: early breeders tended to select more precocious wheat than available on average in quadrats of 5 km<sup>2</sup>. Early breeders were thus able to discriminate wheat quality at both large and fine spatial scales. In contrast, by definition, late breeders reproduce later in the season when the relative precocity of wheat may no longer be a good proxy of habitat quality (i.e. wheat height is more homogeneous). Additionally, since Montagu's harrier is a semi-colonial species, late breeders may be attracted by earlier ones at large scale (i.e. conspecific attraction) but may be unable to

discriminate patch quality at small scales (Valone 2007). Besides they may be constrained to nest in different patches than first breeders, because of the existence of some competition between pairs (for mates, etc.; Mougeot et al. 2001, Arroyo et al. 2001) but still nest in patches close to first breeders to keep the benefits of coloniality but to the detriment of patch quality (Gillis and Bretagnolle [c], in prep.).

This study underlines that considering multiple spatio-temporal scales could lead to complementary conclusions (Levin 1992, Rettie and Messier 2000) but also demonstrates the importance to define an appropriate scale to detect habitat selection processes. Indeed, we detected different patterns and mechanisms of habitat selection depending on the spatio-temporal scale considered. Since factors with greater potential to reduce individual fitness are more likely to be avoided at large spatio-temporal scale (Rettie and Messier 2000), conservation of the endangered Montagu's harrier should rather concentrate on areas with precocious wheat to maximize individual fitness.

Remote sensing technology may be recommended to detect patterns at relative broad scale but also finer scales. However, future development of the method may be to assess patch quality at field scale since our present method (i.e. 250 m pixel scale) actually erased some of the wheat precocity variability (one pixel could contain several wheat fields of different phenology). Such developments should provide considerable new perspectives to ecologists, in particular in studies of habitat selection in farmland landscapes.

### *Acknowledgements*

KLR performed most of statistical analysis while MG, SC and MW treated and provided remote sensing data. Many people helped collecting data on land use and harriers in the field and are kindly thanked. ANR BIODIVAGRIM and ANR-ERANET ECOCYLCES partly funded this study. HG was funded through a PhD from the ED "Diversité du Vivant", University of Paris VI.

# C. Synthèse générale, discussion et perspectives





L'objectif de cette thèse était d'examiner la sélection de l'habitat, et plus particulièrement du site de nidification chez le Busard cendré dans le contexte actuel du changement global en allant des patrons aux processus sous-jacents. Pour cela nous avons utilisé différentes échelles temporelles (intra- et inter-annuelles) et spatiales. Dans ce dernier chapitre, nous commencerons par rappeler brièvement les principaux résultats obtenus. Dans un deuxième temps, nous mènerons une réflexion quant à l'avenir du Busard cendré dans les milieux agricoles intensifs dans le contexte du changement global. Enfin, dans un troisième et dernier temps, nous discuterons de la pertinence des moyens de conservation du Busard cendré actuellement mis en place dans le contexte du changement global avant de proposer la mise en place de moyens pouvant paraître plus adaptés.

## **C.I. PRINCIPAUX RESULTATS OBTENUS**

Dans le premier chapitre, nous nous sommes intéressés aux processus sous-jacents de la sélection de hauteur de végétation au nid chez les oiseaux nichant au sol. Les principales pressions de sélection s'exerçant sur le choix d'une hauteur de végétation chez ces espèces dont fait partie le Busard cendré sont le risque de prédation et d'insolation des œufs et des poussins. Indépendamment de la croissance de la végétation, l'importance relative de ces deux pressions varie au cours d'une saison de reproduction (car le risque de prédation est constant alors que le risque d'insolation augmente). Le choix d'une hauteur de végétation comme protection contre la prédation et/ou l'insolation dépend donc de la date de ponte des individus et de leurs potentielles stratégies alternatives de protection du nid (*article 1*).

Dans le deuxième chapitre, nous avons dégagé les patrons globaux de sélection de hauteur de végétation au nid chez le Busard cendré et les mécanismes écologiques qui la modulent : phénologie de la végétation, abondance de proies et interactions sociales. Nous avons également examiné les conséquences de cette sélection sur la fitness. Les espèces se reproduisant en milieu agricole, tel que le Busard cendré, font face à un milieu particulièrement changeant lors d'une saison de reproduction du fait de la croissance rapide des cultures. Les individus se reproduisant en début de saison quand les hauteurs sont globalement faibles sont donc plus sélectifs et cherchent les rares parcelles de blé ayant une hauteur acceptable. Les individus tardifs semblent quand à eux moins sélectifs car en fin de saison la majorité des parcelles atteignent la hauteur qu'ils préfèrent (*article 2*).



Nous avons ainsi identifié les composantes de l'habitat responsables des variations inter-annuelles de la sélection de hauteur de végétation (*article 2*):

- i) la phénologie du blé : plus le blé est précoce moins les busards sont sélectifs
- ii) l'abondance de proies : plus l'abondance de campagnols est importante plus les busards sont sélectifs
- iii) la densité de conspécifiques : plus un individu a de voisins moins il est sélectif sur la hauteur.

Comme prédit, la hauteur choisie influence le taux de prédation au stade œuf et donc la fitness des individus. Cependant, l'aspect social (le nombre de voisins et la qualité relative des couples) est crucial aussi bien du point de vue de la sélection de hauteurs (*article 2 & 3*) que du taux de prédation au stade œuf. Contrairement à ce que l'on aurait pu penser, la colonialité augmente le risque de prédation au stade œuf (*article 2*).

Dans le troisième chapitre, nous nous sommes intéressés aux patrons temporels d'installation des individus dans une colonie suivant la qualité des parcelles et la présence de congénères. Les individus précoces donc de meilleure qualité s'appuient sur leur information personnelle pour choisir une parcelle et donc une hauteur de végétation favorable. Cette utilisation de l'information personnelle pour la sélection d'une parcelle diminue avec le rang d'arrivée du couple dans la colonie au profit de l'utilisation de l'information publique (*article 3*). Les premiers couples qui s'installent, semblent donc définir la position des futures colonies (*article 3*).

Enfin, dans le quatrième et dernier chapitre, nous avons examiné la distribution des nids à différentes échelles spatiales de 2001 à 2011 en lien avec la distribution spatiale et temporelle d'un indice de précocité du blé (proxy de la qualité du blé). A l'échelle de la zone d'étude, la position de tous les nids dépend de la distribution spatiale des précocités des blés (qui dépend en partie des températures de surface et de la pédologie) alors qu'à plus fine échelle, seule la position des nids des individus précoces dépend de cette distribution. La distribution spatiale des précocités de blé étant relativement stable d'une année à l'autre, la position des nids et donc des colonies présente de faibles variations inter-annuelles (*article 4*).

Les mécanismes identifiés soulignent l'importance de considérer l'effet des trois composantes de l'habitat (physique, biologique et sociale) afin de comprendre les variations temporelles de la sélection du site de nidification des espèces et plus particulièrement chez les espèces coloniales ou semi-coloniales comme le Busard cendré. Un système écologique





présente généralement des variabilités selon l'échelle spatiale, temporelle et organisationnelle considérée (Levin 1992). Dans ce travail de thèse, notre approche multi-échelle à la fois temporelle et spatiale, a permis non seulement de mettre en évidence des variabilités dans les patrons de sélection de hauteur et dans la distribution spatiale des nids, mais aussi de comprendre les mécanismes sous-jacents à ces variations. Ce travail attire également l'attention sur la nécessité d'utiliser des données à long terme présentant des conditions biotiques et abiotiques contrastées afin d'éviter toute interprétation hâtive et faussée.

## **C.II. QUEL AVENIR POUR LE BUSARD CENDRE DANS LE CONTEXTE DU CHANGEMENT GLOBAL?**

Ce travail de thèse nous a permis d'identifier les principaux mécanismes impliqués dans la sélection d'habitat du Busard cendré mais également des tendances sur l'évolution de l'habitat et des pressions de sélection, potentiellement attribuables au changement global. Les résultats obtenus nous permettent une meilleure compréhension des exigences de cette espèce vis à vis de son habitat et sont donc les premiers pas vers la prédiction de l'avenir de l'espèce dans le contexte du changement global. Dans cette partie, nous allons donc, dans un premier temps, mener une réflexion quant à l'avenir du busard cendré en milieu agricole intensif si les tendances actuelles persistent. Dans un deuxième temps, nous discuterons du rôle potentiel du changement global dans les variations temporelles observées.

### **C.II.1. Si les tendances se confirment...**

Des tendances sur les 16 dernières années ont d'ores et déjà été mises en évidence concernant l'habitat physique et biologique du Busard cendré en période de reproduction (*article 2*). En effet, les blés sont de moins en moins hauts mais leur phénologie, variable d'une année sur l'autre, ne présente pas de tendance sur ces 16 dernières années (*article 2*). Parallèlement, l'abondance de campagnols, qui présentait une dynamique cyclique de forte amplitude jusqu'au début des années 2000, est depuis moins variable (atténuation de l'amplitude des cycles) avec des abondances moyennes relativement faibles. Cette moindre abondance de campagnols n'incite pas les busards à s'investir fortement dans la reproduction et donc à sélectionner des hauteurs de blé importantes. Suite à ces deux phénomènes



(diminution des hauteurs de blé et des ressources alimentaires), les Busards nichent dans des hauteurs de blé de plus en plus basses et cela en dépit du fait qu'ils sélectionnent des hauteurs supérieures au disponible (*article 2*). Ils sont donc davantage soumis aux risques de prédation et d'insolation des œufs, ce qui conjointement entraîne une diminution du succès à l'éclosion (*article 1 & 2*). Si les tendances sur les hauteurs de blé et l'abondance de campagnols persistent, les Busards nichant dans ce type de culture risquent de voir leur fitness diminuer.

L'écrasement des cycles de campagnols s'accompagne d'une augmentation de l'hétérogénéité de leur distribution entre les types de culture (figure C.1). Les campagnols sont alors davantage concentrés dans les milieux pérennes (surtout les luzernes; Figure C.1, Pinot A. *Com. Pers.*).

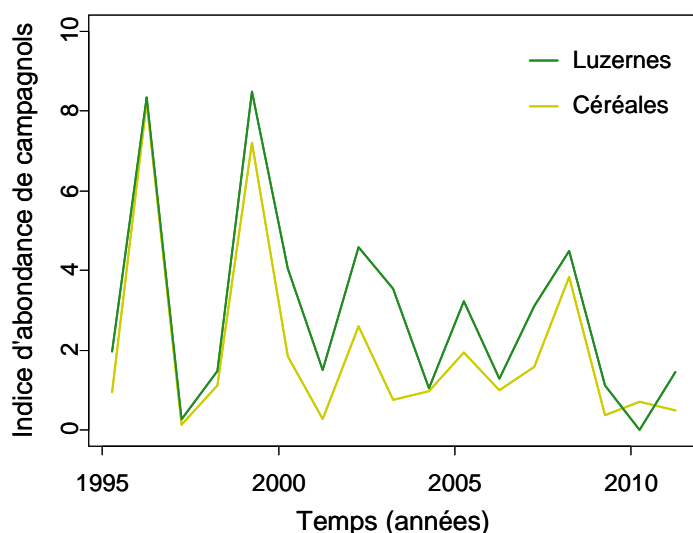


Figure C.1: Evolution des différences d'abondance de campagnols au printemps entre les milieux pérennes (luzernes) et les céréales (Source : Pinot A.)

La diminution des hauteurs atteintes par le blé et la diminution de l'abondance des proies dans les céréales pourraient expliquer le fait que les couples les plus précoces s'installent de plus en plus dans des milieux pouvant être qualifiés « de substitution » tels que les cultures pérennes (luzerne et ray-grass) ou les milieux naturels (Figure C.2). Les cultures pérennes semblent en effet être de meilleure qualité que le blé (en termes de structure de végétation : densité plus importante) en début de saison (*article 3*) et concentrent, en outre, des abondances importantes en campagnols (Pinot A. *Com. Pers.*). Cependant, ces milieux subissent des fauches extrêmement précoces comparées aux dates de moisson des céréales. En effet, les premières coupes ont lieu dès le mois de mai, bien avant l'envol des jeunes. Les nids en luzerne sont donc souvent voués à l'échec. L'utilisation de ces milieux pourrait alors constituer un piège écologique.

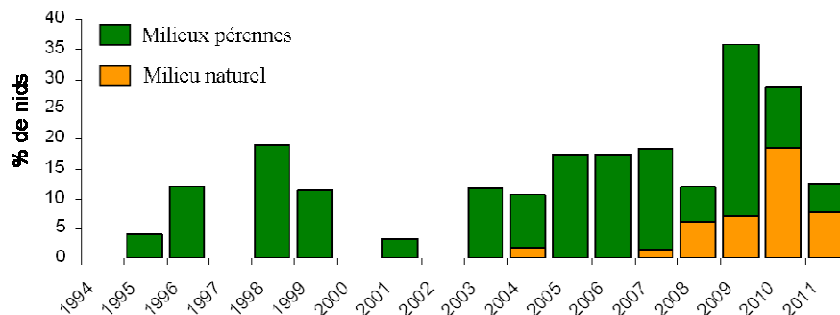


Figure C.2 : Pourcentage de nids de Busard cendré dans les milieux « de substitution » entre 1994 et 2011. L'utilisation de ces milieux est en augmentation (corrélation de Spearman :  $r = 0.64$ ,  $p = 0.004$ ).

D'autre part, une partie des individus précoces choisissent depuis quelques années, sur notre site d'étude, le retour en milieu naturel dans une forêt en régénérescence (suite à la tempête de 1999 mais également à l'exploitation forestière), juxtaposée à la zone d'étude (Forêt de Chizé) (figure C.3). En milieu forestier, la contrainte d'accessibilité au nid est accentuée (Limiñana et al. 2006). Les busards tendent donc à nicher dans les zones plus basses que la moyenne (ronciers, arbustes, herbacées, voir Limiñana et al. 2006, Limiñana et al. 2011 pour une étude en milieu naturel en Espagne). Cependant, les hauteurs au nid restent plus importantes (moyenne  $\pm$  SD :  $104 \pm 29$  cm) qu'en milieu céréalier (données non publiées mais voir également Limiñana et al. 2006). Au détriment de la plaine céréalière, le milieu naturel situé à proximité de cette dernière (toujours utilisée comme territoire de chasse ; données non publiées) deviendrait donc de plus en plus favorable.



Figure C.3 : Localisation de la forêt de Chizé (milieu naturel utilisé par les Busards cendrés) par rapport à la zone d'étude

Comme évoqué dans le paragraphe précédent, les cultures pérennes et les milieux naturels sont principalement utilisés par les couples précoces (figure C.4). Or, les dates



moyennes de ponte des Busards cendrés semblent être de plus en plus précoces sur notre zone d'étude (figure C.5). Si les tendances se confirment, la proportion d'individus utilisant ces milieux dit « de substitution » devrait donc croître. L'avancée des dates de ponte est un phénomène observée chez de nombreuses espèces d'oiseaux (Dunn et al. 2010). Chez le Busard cendré, il est connu que la date de ponte est fortement liée à l'abondance de campagnols au printemps : les dates de pontes sont précoces quand l'abondance de campagnols est élevée (Millon and Bretagnolle 2008). L'abondance de campagnols au printemps étant, au contraire, globalement en diminution sur la période d'étude, elle ne peut justifier ces avancées de dates de ponte. Une autre explication aurait pu être l'avancée des phénologies de blé mais aucune tendance n'est observable sur notre zone d'étude. Des modifications de l'habitat physique et biologiques de la zone d'étude ne semblent donc pas être responsables de l'avancée de la phénologie de reproduction de l'espèce. Un effet direct du changement climatique sur la physiologie de reproduction des individus (Goutte 2010) ou des modifications des conditions sur les sites d'hivernages ou lors de migration (Lehikoinen and Sparks 2010) sont envisageables et à étudier comme explications plausibles de cette avancée.

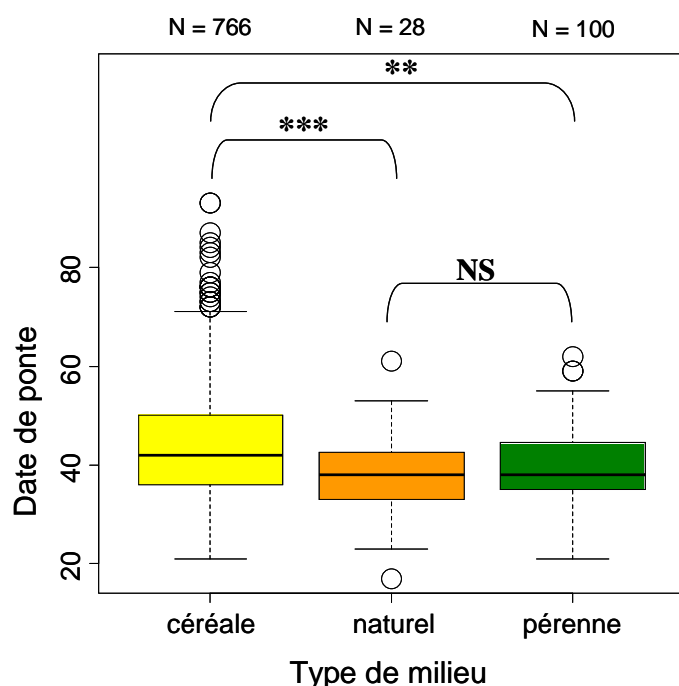


Figure C.4 : Dates de pontes (en jour julien à partir du 1<sup>er</sup> avril) des Busards cendré dans notre zone d'étude (Zone Atelier Plaine et Val de Sèvre et forêt de Chizé) suivant le type de milieu choisi pour la nidification. Les dates de pontes moyennes ( $\pm$  SD) sont les suivantes :  $44.3 \pm 11.5$  dans les céréales,  $39.8 \pm 7.8$  dans les milieux pérennes et  $37.7 \pm 9.2$  en forêt. Les différences de moyennes de dates de pontes entre les 3 milieux ont été testé à l'aide d'un test t de Student (NS : non significatif, \*\* :  $0.01 < p < 0.001$ , \*\*\*  $p < 0.001$ ).

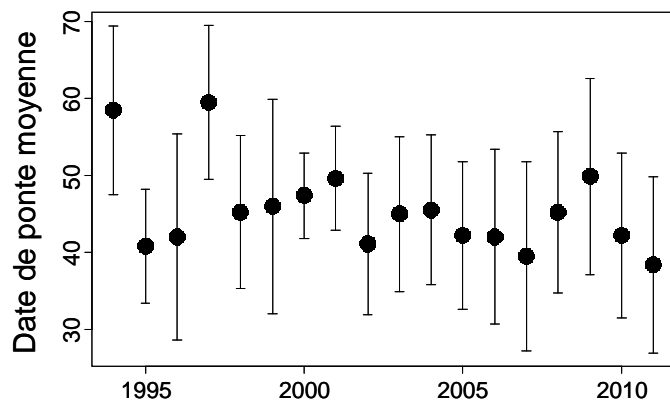


Figure C.5 : Evolution des dates moyennes de ponte ( $\pm$  SD) du Busard cendré tous milieux confondus de 1994 à 2011 sur la zone d'étude (forêt comprise). Globalement les dates de pontes moyennes ont tendances à être de plus en plus précoces (Corrélation de Spearman :  $r = -0.5$ ,  $p = 0.05$ )

Au vu de nos résultats et de la discussion menée ci-dessus, il paraît extrêmement complexe de prédire l'avenir du Busard cendré car les effets confondants et les interactions entre compartiments de l'habitat sont multiples. Des tendances sur la période d'étude sont observées mais les origines de celles-ci ne sont pas réellement identifiées. Le changement global pourrait être mis en avant comme explication plausible.

### **C.II.2. Le changement global, cause des variations temporelles observées ?**

Dans ce travail de thèse, nous avons mis en évidence les mécanismes environnementaux responsables des variations des patrons de sélection du site de nidification et des performances reproductives du Busard cendré. Nous avons également discuté de l'influence potentielle du changement global sur ces mécanismes. Cependant, nous n'avons pas établi de liens directs (ou indirects) entre les patrons observés et le changement global. Il s'agit donc de la prochaine étape et nous disposons de certaines données concernant le climat et les pratiques agricoles. Cette partie est donc consacrée à une exploration de l'influence du climat et des pratiques agricoles sur l'habitat physique et biologique du busard cendré.

Le changement global pourrait, en effet, être une des causes de variation de phénologie et de hauteurs du blé mais aussi de l'abondance de campagnols (Arroyo et al. 2002). La somme des températures et des précipitations tout au long de l'année est un des facteurs clés pour la croissance des cultures (Geslin 1944). Cependant, les données climatiques dont nous disposons (station de Niort) présentent des variations annuelles mais pas de tendances générales (figure C.6a & b) ces 20 dernières années. Ce laps de temps paraît relativement court pour dégager des tendances climatiques. Ces variations annuelles de température et de



précipitations pourraient toutefois expliquer l'absence de tendance dans la phénologie des blés. Elles n'expliquent cependant ni les tendances à la diminution des hauteurs de blés et des abondances de campagnols ni l'avancée des dates de ponte du Busard cendré. L'exploration approfondie de ces données climatiques (tendances saisonnières) ainsi que l'étude de l'interaction entre températures et précipitations pourraient toutefois partiellement expliquer les tendances observées dans l'habitat. Le changement global n'est pas synonyme de changement climatique mais intègre également les changements d'utilisation des sols, de pratiques agricoles. La croissance des blés ainsi que la hauteur atteinte par ceux-ci découlent également des itinéraires techniques suivis par les acteurs principaux des territoires agricoles : les exploitants agricoles. Des différences de dates de semis, de variétés de blé, de quantités d'engrais utilisées, d'arrosage des parcelles et d'utilisation de raccourcisseurs de croissance peuvent effectivement influencer les hauteurs de blé rencontrés par les busards. Il est également connu qu'une interaction entre le climat et les pratiques agricoles existe (Thuiller 2003). La diminution des hauteurs de blé et l'atténuation des cycles d'abondance de campagnols résultent certainement de cette interaction. Il est plus difficile de disposer de données sur l'évolution temporelle des pratiques agricoles à l'échelle locale. Il semble toutefois nécessaire et indispensable de récolter de telles données (à partir du cahier des charges des exploitants ou auprès de coopératives agricoles) afin de pouvoir distinguer les effets respectifs des variations du climat et des pratiques agricoles sur la phénologie du blé, l'abondance de campagnols et donc sur la sélection de hauteur de végétation au nid et la fitness des Busards cendrés.

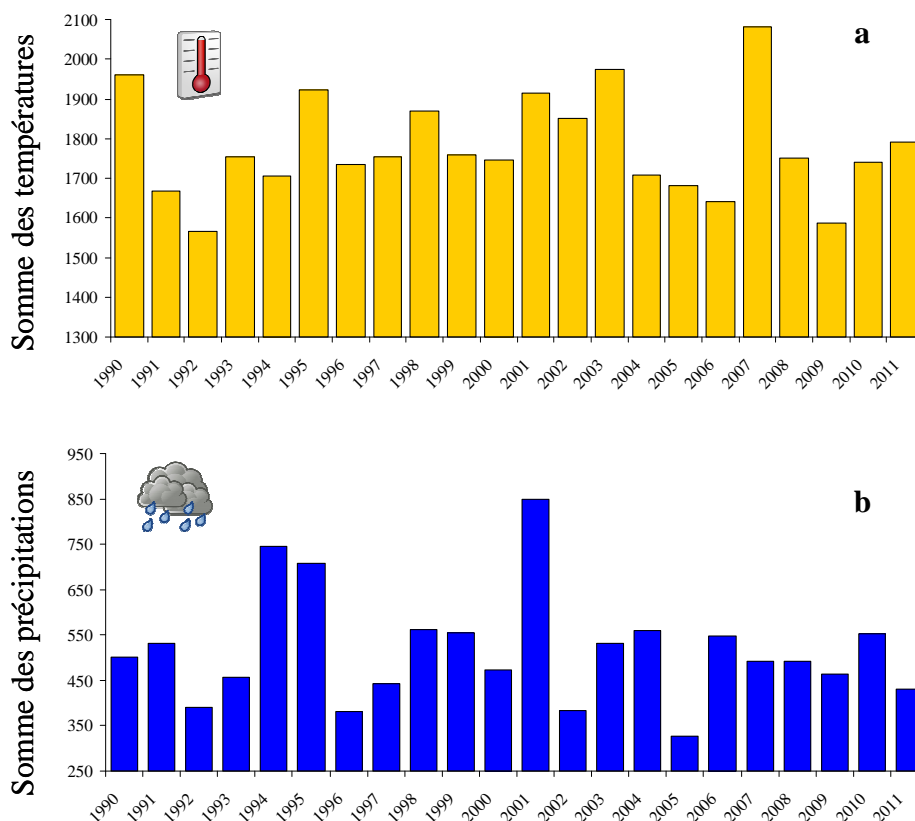


Figure C.6 : Sommes des températures (a) et des précipitations (b) de 1990 à 2011 au niveau de la station de Niort (station la plus proche de la zone d'étude). La somme considérée est du 1<sup>er</sup> octobre de l'année précédente (correspondant à la période de semis du blé) au 30 avril de l'année en question (correspondant aux 1<sup>ères</sup> installations de Busards cendrés)

### **C.II.3. Une prochaine étape : Modéliser pour prédire**

Comprendre l'impact des changements climatiques et d'usage des sols futurs sur les populations animales fait l'objet d'un intérêt croissant et les études visant à prédire la distribution et la persistance des espèces dans ce contexte sont de plus en plus nombreuses. Cette étape prédictive nécessite l'identification et la compréhension des mécanismes impliqués dans la sélection d'habitat, ses variations et ses conséquences sur la fitness. La conception de modèles prédictifs suivant différents scénarii climatiques et différents itinéraires techniques, incluant les mécanismes identifiés lors de cette thèse mais également ceux déjà connus (résumé dans la figure C.7) semblerait être une suite logique à ce travail afin de prédire l'avenir du Busard cendré en milieu agricole intensif.

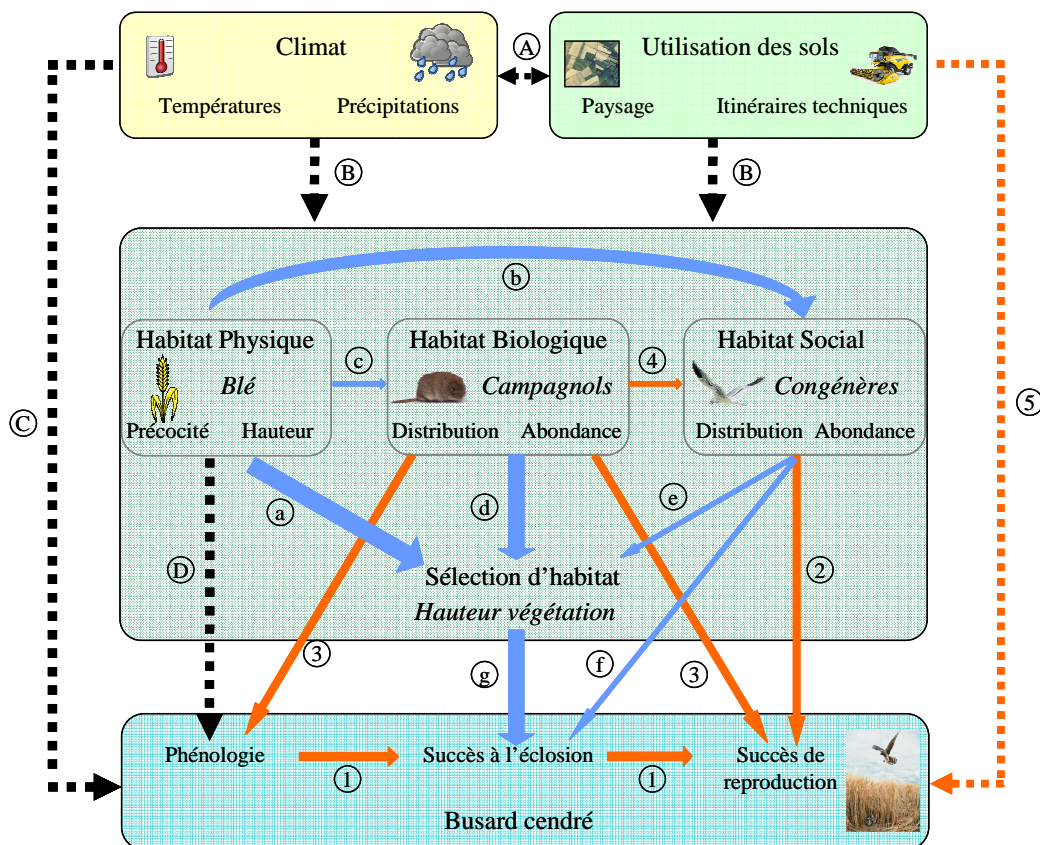


Figure C.7: Schéma récapitulatif des relations connues (en orange et numéro), inconnues (en pointillés noirs et lettres majuscules) et identifiées dans cette thèse (en bleu et lettres minuscules) entre les compartiments du changement global, de l'habitat et de la reproduction du Busard cendré. La largeur des flèches bleues est proportionnelle à l'importance des relations.

- 1- Les individus précoces sont plus productifs en termes de poussins et ont un succès de reproduction plus élevé (Millon et al 2008)
- 2- La présence de congénères permet de diminuer le taux de prédation au stade « poussin » (Arroyo et al. 2001)
- 3- Les années de fortes abondances de campagnols: les individus sont plus précoces et ont un succès de reproduction plus élevé (Millon et al 2008)
- 4- Les années de fortes abondances en campagnols, la densité de nid est plus importante et les nids plus agrégés (de Cornulier 2005)
- 5- Sans protection, les moissons détruiraient 60% des nids (Arroyo et al. 2002). Nous ne connaissons pas l'influence indirecte des autres travaux agricoles sur le busard cendré.
- a- Une phénologie tardive et des hauteurs faibles du blé rendent les busards plus sélectifs (article 2)
- b- Les patches de blés les plus précoces accueillent les colonies de Busards (article 4)
- c- La phénologie du blé semble en lien avec l'abondance de campagnols (article 2, à préciser davantage)
- d- Une forte abondance de campagnols incite les Busards à investir davantage dans la reproduction et donc à être plus sélectif sur la hauteur de végétation (article 2)
- e- Les couples arrivant dans des colonies importantes sont moins sélectifs sur la hauteur de végétation (article 2 & 3)
- f- Plus la colonie est grande plus le risque de prédation au stade œuf est élevé (article 2)
- g- Les individus ayant choisi une hauteur de végétation au nid importante diminuent le risque de prédation au stade œuf et augmentent par conséquent le succès à l'éclosion (article 2)
- A- Les interactions entre pratiques agricoles et changement climatique
- B- Effets respectifs du changement climatique et de l'agriculture sur les composantes de l'habitat
- C- Effets directs du changement climatique local (physiologie de reproduction) ou global (modifications des sites d'hivernages ou des conditions de migration)
- D- La phénologie du blé ne semble pas influencée la phénologie de reproduction. Cette relation est toutefois à approfondir





### **C.III. CONSERVATION DU BUSARD CENDRE EN MILIEU AGRICOLE DANS LE CONTEXTE DU CHANGEMENT CLIMATIQUE**

Les espèces inféodées aux milieux agricoles sont particulièrement exposées à tout changement potentiel de leur habitat lié aux activités humaines. Les menaces auxquelles doivent faire face ces espèces sont aujourd'hui accentuées par l'intensification de l'agriculture mais aussi par le changement climatique. De forts enjeux de conservation sont donc en cours dans ces milieux. De nombreuses mesures de conservation (telles que les mesures agri-environnementales) ont été mis en place afin de contrer le déclin des oiseaux agricoles. Avant ce travail de thèse, les principales menaces identifiées pesant sur le Busard cendré étaient la diminution de l'abondance de leur ressource alimentaire (lié à l'intensification et aux changements d'utilisation des sols, Arroyo et al. 2002) et les destructions de nichées par les moissons (Arroyo et al. 2002, Limiñana et al. 2011). Des mesures de conservation (décrites ci-dessous) ont été mises en place afin de contrer ces menaces. Cependant, ces mesures sont et seront-elles efficaces dans un contexte de changement global ? C'est la question à laquelle nous tenterons de répondre dans un premier temps. A la lumière des nouveaux éléments apportés dans cette thèse, nous tenterons dans une seconde partie de proposer des mesures de conservation du Busard cendré en milieu agricole, potentiellement adaptées pour faire face au changement global.

#### **C.III.1. Mesures de conservation actuelles et efficacité face au changement global**

##### **C.III.1.i. Un dispositif de protection des nids**

Depuis 1994, sur la zone d'étude, d'importantes ressources humaines mais aussi économiques sont investies chaque année dans la protection des nids de Busards cendrés au moment de la moisson des céréales (Arroyo et al. 2002). La pose de grillage (figure C.8) avant la moisson est une mesure de conservation largement utilisée en France et dans de nombreux pays européens pour protéger les jeunes Busards cendrés mais également les



Busards Saint-Martin *Circus cyaneus* et les Busards des roseaux *Circus aeruginosus* nichant en milieu agricole. Avec la collaboration des exploitants agricoles, ces grillages sont installés le plus tard possible pour éviter l'abandon du nid par la femelle mais avant la moisson afin d'éviter la destruction des nids lors du passage de la moissonneuse mais aussi afin d'éviter une prédation terrestre accrue (chien, chat, renard) provoquée par une détection du nid facilitée dans un champ de chaume. L'efficacité de cette mesure est incontestable car près de 60% des nids sont détruits en l'absence de cette mesure (Arroyo et al. 2002). Cependant, nous sommes en droit de nous demander si cette mesure est réellement pérenne dans un contexte de changement global. L'augmentation des échecs liés à des hauteurs de végétation trop basses et à la diminution d'abondance de campagnols est en effet à prévoir. Suite la diminution des hauteurs de blé choisis, de plus en plus de nids sont prédatés au stade œuf. La pose d'un grillage au stade œuf n'aurait aucune efficacité face aux principaux prédateurs des œufs de Busards, les corvidés. Cette mesure ne sera plus si performante et rentable pour la persistance de l'espèce dans le contexte du changement global si les tendances sur les abondances de campagnols et sur les hauteurs de blé (et donc sur la prédation des œufs) se confirment. Comme précisé par Arroyo et al. (2002), la manière la plus efficace et rentable de protéger le Busard cendré serait de mettre en place des mesures à l'échelle plus large de l'habitat et non du nid.



Figure C.8 : photographies d'un nid protégé par un grillage avant (a- photo : © Serge Paris) et après moisson (b- photo : © Jean-Luc Bourrioux)

### C.III.1.ii. Une Zone de Protection Spéciale

La zone d'étude est en grande partie couverte par une Zone de Protection Spéciale (la ZPS Niort-Sud Est; figure C.9). Les zones de protection spéciale ont été créées en application



de la directive européenne 79/409/CEE (« directive oiseaux ») relative à la conservation des oiseaux sauvages. Cette ZPS a été désignée entre autres pour son importance pour les populations d'Outardes canepitières *Tetrax tetrax*. La France a choisi la méthode de contractualisation volontaire pour atteindre les objectifs de protection identifiés (par un document d'objectifs visant à diagnostiquer et orienter la gestion des sites Natura 2000). Dans ce cadre, des mesures agri-environnementales (MAE) basées sur des contrats avec les exploitants agricoles, ont été mises en place sur la ZPS Niort-Sud Est. Ces mesures visent à favoriser le retour des prairies et des pratiques de gestion favorables aux criquets, ressources alimentaires de l'Outarde canepetière (amélioration des sites de reproduction, d'alimentation et d'élevage des jeunes). Cette mesure n'est évidemment pas ciblée sur le Busard cendré. Cependant, en l'absence de MAE « Busard cendré », la favorisation des milieux pérennes (milieu refuge pour les campagnols) pourraient avoir un impact positif sur l'abondance des campagnols et donc sur les Busards. L'outarde canepetière constituerait, dans ce cas, une espèce « parapluie » (Lambeck 1997). Cependant, ces mesures ne contrent en rien la diminution observée de la qualité (hauteurs) des blés pour la nidification des Busards cendré.

Aucun moyen de conservation actuel ne semble en mesure d'assurer la persistance du busard cendré en milieu agricole face aux changements environnementaux en cours.

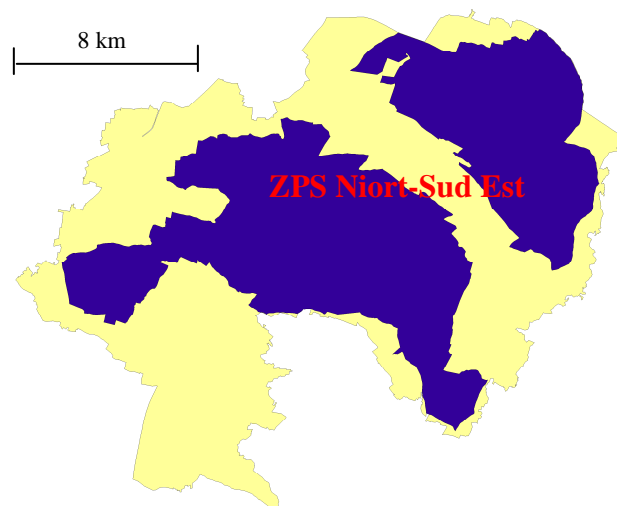


Figure C.9 : Zone Atelier Plaine et Val de Sèvre (jaune & bleu) et Zone de Protection Spéciale Niort-Sud Est (bleu).

### **C.III.2. Propositions de mesures pérennes adaptées au changement global:**

Les mesures de conservation étant coûteuses et les ressources financières limitées, l'efficacité des mesures doit être avérée afin d'optimiser l'utilisation du budget disponible



(Arroyo and Bretagnolle 2000). Or, comprendre la puissance des relations entre l'habitat, la distribution et le succès de reproduction d'une espèce est crucial pour la mise en place de programmes de conservation efficaces (Limiñana et al. 2011). Nous avons dans cette thèse apportée des éléments essentiels qui pourraient contribuer à cibler davantage les mesures de conservation du Busard cendré à travers son habitat. A la vue de nos résultats et de la discussion menée plus haut, deux options se dégagent. La première consisterait à favoriser la colonisation, déjà observable, des milieux naturels. La seconde à créer une mesure agri-environnementale ciblée sur le Busard cendré.

### **C.III.2.i. Favoriser la colonisation des milieux naturels**

Nous l'avons discuté, les mesures actuelles se concentrent sur les habitats agricoles de l'espèce. Cependant, les milieux naturels présentent l'avantage de ne pas subir l'influence des pratiques agricoles, notamment la moisson. Nous avons précédemment mentionné la colonisation récente de la forêt par la population présente sur notre zone d'étude. Favoriser cette colonisation paraît donc être une des possibilités pour la pérennité de l'espèce (également mentionné par Arroyo et al. 2002). Cependant, cette alternative nécessiterait de limiter les activités forestières pendant la saison de reproduction et d'appliquer une gestion régulière de la végétation naturelle en période d'hivernage des oiseaux afin de maintenir un couvert favorable à la nidification. Dans un premier temps, les zones déjà colonisées devraient être gérées sur une surface assez large (environ 1000 m de rayon) afin de favoriser la colonialité. Dans un second temps, la création d'autres zones favorables pourraient être envisagée enfin d'attirer de nouvelles colonies. Afin de maximiser les chances de réussite de tels programmes, les mesures devraient évidemment s'appuyer sur des études de sélection d'habitat en milieu naturel. De telles études sont déjà en partie disponibles (voir Limiñana et al. 2006, Cormier et al. 2008, Wiacek 2008, Limiñana et al. 2011). Il reste cependant une inconnue non négligeable : où ces couples vont-ils chasser ? Basé sur les pelotes de rejection trouvées au nid, il est possible de reconstituer le régime alimentaire de ces couples (Salamolard et al. 2000). Dans le cas où ces individus persisteraient à chasser dans la plaine céréalière, la diminution des ressources alimentaires en milieu agricole resterait problématique pour le succès de reproduction du Busard cendré.



### **C.III.2.ii. Création d'un habitat idéal et Mise en place d'une MAE ?**

Les propositions suivantes découlent d'une réflexion centrée sur la création d'un habitat idéal pour le Busard cendré en plaine agricole intensive suivant les éléments mis en évidence dans cette thèse. La faisabilité de ces mesures est par la suite discutée.

Idéalement, les mesures devraient considérer les trois composantes de l'habitat en favorisant des hauteurs de blé importantes, une augmentation de l'abondance de campagnols et en prenant en compte le caractère colonial de l'espèce. Il semblerait que ces mesures devrait se concentrer sur les colonies relativement fixes d'une année sur l'autre et donc dans les zones où le blé est plus précoce (zones identifiées dans l'*article 4*). Dans ces larges zones (750 à 1500 mètres de diamètre), des variétés de blés précoces, peu gourmandes en eau et atteignant rapidement la hauteur favorite du Busard cendré (80 cm) seraient idéalement à privilégier afin de fournir une protection optimale contre la prédation aérienne et l'insolation tout en maintenant une accessibilité facile aux parents. Cependant, des variétés précoces sont souvent récoltées plus tôt. Les moissons devraient donc être retardées afin de permettre l'envol des jeunes. Les causes exactes des cycles de campagnols et de leur changement ne sont pas encore élucidées. Une meilleure répartition spatiale des milieux constituant des refuges pour les campagnols en hiver : les milieux pérennes, pourraient, cependant, favoriser la colonisation des blés (milieu de chasse favori des busards ; Lecoustre 2009) par les campagnols et ainsi relancer les cycles (Pinot A., *Com. Pers*). Les milieux pérennes devraient donc se répartir de manière régulière sur l'ensemble des zones spécifiés précédemment. Enfin, nous avons vu qu'il est important de considérer l'aspect social de cette espèce. Pour ce faire, il semblerait intéressant de favoriser des patchs de blés de superficie importante afin de permettre aux couples de moins bonne qualité (et donc non capables de discriminer la qualité relative des patchs), de s'installer dans des bons patchs tout en maintenant une certaine distance avec ses propres voisins (afin d'éviter la compétition).

La description faite ci-dessus constitue un habitat « idéal » pour la nidification du Busard cendré. Cependant, l'accumulation des contraintes (variétés, dates de moisson, taille des parcelles) rend sa réalisation délicate. Il paraît en effet difficile de créer un cahier des charges acceptable pour l'agriculteur tout en limitant le montant de la rémunération calculée sur la base des surcoûts et pertes occasionnés par les engagements. De plus, la plupart des mesures proposées (mise à part la mise en place de milieux pérennes) pourrait s'avérer nuisible au reste de la communauté biologique. Des mesures simples et non nuisibles pour les autres



espèces devrait donc être favorisées telles que l'utilisation de variétés de blé atteignant des hauteurs importantes, l'incitation à ne pas utiliser de raccourcisseurs et le retard des moissons. Concernant l'abondance et la disponibilité des campagnols, les MAE actuellement en place et en développement pourraient suffire. Cependant une étude approfondie des liens entre abondance et répartition des habitats pérennes et abondance de campagnols devra être conduite pour valider l'effet supposé positif des MAE.



# D. Références bibliographiques



La Biblio, c'est la vie, BiblioVie...

Kévin Le Rest





- Allen, T. and Hoekstra, T. 1993. Toward a unified ecology. – Columbia Univ Pr.
- Ar, A. and Sidis, Y. 2002. Nest microclimate during incubation. – OXFORD ORNITHOLOGY SERIES 13: 143–160.
- Arroyo, B. 1998. Effect of diet on the reproductive success of Montagu's Harrier *Circus pygargus*. – Ibis 140(4): 690–693.
- Arroyo, B. 1999. Copulatory behavior of semi-colonial Montagu's Harriers. – Condor pp. 340–346.
- Arroyo, B. and Bretagnolle, V. 2000. Evaluating the long-term effectiveness of conservation practices in Montagu's Harrier *Circus pygargus*. – Raptors at the risk pp. 403–408.
- Arroyo, B., Bretagnolle, V. and Leroux, A. 2007. Interactive effects of food and age on breeding in the Montagu's Harrier *Circus pygargus*. – Ibis 149(4): 806–813.
- Arroyo, B., García, J. and Bretagnolle, V. 2002. Conservation of the Montagu's harrier *Circus pygargus* in agricultural areas. – Animal Conservation 5(04): 283–290.
- Arroyo, B.; García, J. & Bretagnolle, V. 2003. Land use, agricultural practices and conservation of Montagu's Harrier. – raptor in a changing environment pp. 449–463.
- Arroyo, B.; García, J. & Bretagnolle, V. 2004. *Circus pygargus* Montagu's harrier. – BWP Update 6(1).
- Arroyo, B., King, J. and Palomares, L. 1995. Observations on the ecology of Montagu's and Marsh Harriers wintering in North-west Sénégal. – Ostrich 66: 37–40.
- Arroyo, B., Mougeot, F. and Bretagnolle, V. 2001. Colonial breeding and nest defence in Montagu's harrier *Circus pygargus*. – Behavioral ecology and sociobiology 50(2): 109–115.
- Assessment, M. 2005. Ecosystems and human well-being. – vol. 5. Island Press.
- Avilés, J., Soler, J. and Pérez-Contreras, T. 2006. Dark nests and egg colour in birds: a possible functional role of ultraviolet reflectance in egg detectability. – Proceedings of the Royal Society B 273(1603): 2821.
- Bakken, G., Vanderbilt, V., Buttemer, W. and Dawson, W. 1978. Avian eggs: thermoregulatory value of very high near-infrared reflectance.. – Science (New York, NY) 200(4339): 321.
- Barbaro, L., Couzi, L. and Bretagnolle, V., Nezan, J. and Vetillard, F. 2008. Multi-scale habitat selection and foraging ecology of the eurasian hoopoe *Upupa epops* in pine plantations. – Biodiversity Conservation 17: 1073–1087.
- Baret, F., Hagolle, O., Geiger, B., Bicheron, P., Miras, B., Huc, M., Berthelot, B., Niño, F., Weiss, M. and Samain, O. 2007. LAI, fAPAR and fCover CYCLOPES global products derived from VEGETATION: Part 1: Principles of the algorithm. – Remote sensing of environment 110(3): 275–286.



- Bayne, E., Hobson, K. and Fargey, P. 1997. Predation on artificial nests in relation to forest type: contrasting the use of quail and plasticine eggs. – *Ecography* 20(3): 233–239.
- Benton, T., Bryant, D., Cole, L. and Crick, H. 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. – *Journal of Applied Ecology* 39: 673–687.
- Blanco, G. and Bertellotti, M. 2002. Differential predation by mammals and birds: implications for egg-colour polymorphism in a nomadic breeding seabird. – *Biological Journal of the Linnean Society* 75(2): 137–146.
- Block, W. and Brennan, L. 1993. The habitat concept in ornithology. – *Current ornithology* 11: 35–91.
- Bollinger, E. 1995. Successional changes and habitat selection in hayfield bird communities. – *The Auk* 112(3): 720–730.
- Boschetti, M., Stroppiana, D., Brivio, P. and Bocchi, S. 2009. Multi-year monitoring of rice crop phenology through time series analysis of MODIS images. – *International Journal of Remote Sensing* 30(18): 4643–4662.
- Bradley, M., Kutz, S., Jenkins, E. and O Hara, T. 2005. The potential impact of climate change on infectious diseases of Arctic fauna. – *International Journal of Circumpolar Health* 64(5): 468.
- Bretagnolle, V. and Gillis, H. 2010. *Predator–prey interactions and climate change*. – Oxford University Press.
- Bretagnolle, V., Villers, A., Denonfoux, L., Cornulier, T., Inchausti, P. and Badenhausser, I. 2011. Rapid recovery of a depleted population of Little Bustards *Tetrax tetrax* following provision of alfalfa through an agri environment scheme. – *Ibis* 153(1): 4–13.
- Brickle, N., Harper, D., Aebischer, N. and Cockayne, S. 2000. Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. – *Journal of Applied Ecology* 37: 742–755.
- Burger, J. 1982. The role of reproductive success in colony-site selection and abandonment in Black Skimmers (*Rynchops niger*). – *The Auk* pp. 109–115.
- Burger, J. 1987. Physical and social determinants of nest-site selection in Piping Plover in New Jersey. – *Condor* pp. 811–818.
- Burhans, D. and Thompson III, F. 1998. Effects of time and nest-site characteristics on concealment of songbird nests. – *Condor* pp. 663–672.
- Butet, A. and Leroux, A. 1993. Effect of prey on a predator's breeding success. A 7-year study on common vole (*Microtus arvalis*) and Montagu's harrier (*Circus pygargus*) in a west France marsh. – *Acta oecologica* 14(6): 857–865.
- Callaway, R.M. & Maron, J. 2006. What have exotic plant invasions taught us over the past 20 years?. – *Trends in Ecology & Evolution* 21: 369–374.



- Campbell, L., Avery, M., Donald, P., Evans, A., Green, R. and Wilson, J. 1997. A Review of the Indirect Effects of Pesticides on Birds. – JNCC Report Joint Nature Conservation Committee, Peterborough, UK. 227.
- Castilla, A., Dhondt, A., Díaz-Uriarte, R. and Westmoreland, D. 2007. Predation in ground nesting birds: an experimental study using natural egg color variation. – *Avian Conservation and Ecology* 2(1).
- Chamberlain, D., Fuller, R., Bunce, R., Duckworth, J. and Shrubbs, M. 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. – *Journal of Applied Ecology* 37(5): 771–788.
- Clark, R. and Nudds, T. 1991. Habitat patch size and duck nesting success: the crucial experiments have not been performed. – *Wildlife Society Bulletin* 19(4): 534–543.
- Clark, R. and Shutler, D. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? – *Ecology* 80(1): 272–287.
- Clarke, R. 1996. Montagu's harrier. – Arlequin Press.
- Claro, J. 2000. Ecologia reproductiva do Tartaranhao-caçador *Circus pygargus* (L.) na região de Évora. Ph.D. thesis, MSc thesis, University of Évora.
- Cody, M. 1985. An introduction to habitat selection in birds. – *Habitat selection in birds* pp. 3–56.
- Colwell, M. 1992. Wilson's Phalarope nest success is not influenced by vegetation concealment. – *The Condor* 94(3): 767–772.
- Conway, C. and Martin, T. 2000. Effects of ambient temperature on avian incubation behavior. – *Behavioral Ecology* 11(2): 178.
- Coolen, I., Bergen, Y., Day, R. and Laland, K. 2003. Species difference in adaptive use of public information in sticklebacks. – *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270(1531): 2413.
- Cormier, J., Fustec, J., Pithon, J. and Choisy, P. 2008. Selection of nesting habitat by Montagu's Harriers *Circus pygargus* and Hen Harriers *Circus cyaneus* in managed heaths: Capsule Montagu's Harriers avoided tree plantations and selected plots with dense heath of intermediate height, while sympatric Hen Harriers preferred afforested or taller plots of heath. – *Bird study* 55(1): 86–93.
- de Cornulier, T. 2005. Composantes de la distribution spatiale d'un prédateur : effets respectifs de l'habitat, des ressources alimentaires et des interactions comportementales. Ph.D. thesis, Université Claude Bernard, Lyon, France.
- Cornulier, T. and Bretagnolle, V. 2006. Assessing the influence of environmental heterogeneity on bird spacing patterns: a case study with two raptors. – *Ecography* 29(2): 240–250.
- Cramp, S. and Simmons, K. 1980. The birds of the western Palearctic, vol. 2.



- Cresswell, W. 1997. Nest predation rates and nest detectability in different stages of breeding in Blackbirds *Turdus merula*. – *Journal of Avian Biology* 28(4): 296–302.
- Crick, H. 2004. The impact of climate change on birds. – *Ibis* 146: 48–56.
- Crick, H. and Sparks, T. 1999. Climate change related to egg-laying trends. – *Nature* 399(6735): 423–423.
- Daan, S., Dijkstra, C., Drent, R. and Meijer, T. 1988. Food supply and the annual timing of avian reproduction. – vol. 19, pp. 392–407.
- Danchin, E., Giraldeau, L., Valone, T. and Wagner, R. 2004. Public information: from nosy neighbors to cultural evolution. – *Science* 305(5683): 487.
- Danchin, E., Boulinier, T. and Massot, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. – *Ecology* 79(7): 2415–2428.
- Danchin, E. and Wagner, R. 1997. The evolution of coloniality: the emergence of new perspectives. – *Trends in Ecology & Evolution* 12(9): 342–347.
- Davis, M. 2003. Biotic globalization: does competition from introduced species threaten biodiversity?. – *BioScience* 53: 481–489.
- Davis, S. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. – *The Condor* 107(3): 605–616.
- Davison, W. and Bollinger, E. 2000. Predation rates on real and artificial nests of grassland birds. – *The Auk* 117(1): 147–153.
- Debouche, C. 1979. Présentation coordonnée de différents modèles de croissance. – *Revue de Statistique Appliquée* 27(4): 5–22.
- Deeming, D. 2002. Avian incubation. – Oxford University Press.
- DeLong, A., Crawford, J. and DeLong, D. 1995. Relationships between vegetational structure and predation of artificial sage grouse nests. – *The Journal of wildlife management* 59(1): 88–92.
- Diggle, P. and Gabriel, E. 2010. Spatio-temporal point processes. – *Handbook of spatial statistics* p. 449.
- Dion, N., Hobson, K. and Larivière, S. 2000. Interactive effects of vegetation and predators on the success of natural and simulated nests of grassland songbirds. – *Condor* 102(3): 629–634.
- Doligez, B., Cadet, C., Danchin, E. and Boulinier, T. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence\* 1. – *Animal Behaviour* 66(5): 973–988.
- Donald, P., Green, R. and Heath, M. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. – *Proceedings of the Royal Society B* 268: 25–29.



- Donald, P.; Sanderson, F.; Burfield, I. & Van Bommel, F. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990-2000. – *Agriculture, ecosystems & environment* 116: 189-196
- Dunn, P., Winkler, D., Møller, A., Fielder, W. and Berthold, P. 2010. Effects of climate change on timing of breeding and reproductive success in birds. – *Effects of Climate Change on Birds* p. 113–128.
- Eggers, S., Griesser, M., Nystrand, M. and Ekman, J. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. – *Proceedings of the Royal Society B: Biological Sciences* 273(1587): 701.
- Evans, A., Smith, K., Buckingham, D. and Evans, J. 1997. Seasonal variation in breeding performance and nestling diet of circl buntings *Emberiza circlus* in England. – *Bird Study* 44: 66–79.
- Ewers, R. and Didham, R. 2005. Confounding factors in the detection of species responses to habitat fragmentation. – *Biological Reviews* 81: 117–142.
- Ferguson-Lees, J. and D.A., C. 2001. *Raptors of the world*. – Houghton Mifflin Harcourt.
- Flynn, D., Gogol Prokurat, M., Nogeire, T., Molinari, N., Richers, B., Lin, B., Simpson, N., Mayfield, M. and DeClerck, F. 2009. Loss of functional diversity under land use intensification across multiple taxa. – *Ecology Letters* 12(1): 22–33.
- Forman, R. 1995. *Land mosaics: the ecology of landscapes and regions*. – Cambridge Univ Pr.
- Fretwell, S. and Lucas, H. 1969. On territorial behavior and other factors influencing habitat distribution in birds. – *Acta biotheoretica* 19(1): 16–36.
- Fuller, R., Gregory, R., Gibbons, D., Marchant, J., Wilson, J., Baillie, S. and Carter, N. 1995. Population declines and range contractions among lowland farmland birds in Britain. – *Conservation Biology* 9 (6): 1425–1441.
- Gatrell, A., Bailey, T., Diggle, P. and Rowlingson, B. 1996. Spatial point pattern analysis and its application in geographical epidemiology. – *Transactions of the Institute of British Geographers* pp. 256–274.
- Geslin, H. 1944. Étude des lois de croissance d'une plante en fonction des facteurs du climat:(Température et radiation solaire.) Contribution à l'étude du climat du blé... – Imprimerie nationale.
- Ghalambor, C. and Martin, T. 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. – *Behavioral Ecology* 13(1): 101.
- Gillis, H., Gauffre, B., Huot, R. and Bretagnolle, V. [a] Vegetation height and egg coloration differentially affect predation rate and overheating risk: an experimental test mimicking a ground-nesting bird. – in review .



- Gillis, H., Millon, A. and Bretagnolle, V. [b]. Where and when to breed do matter: temporal variation in selection of vegetation height at the nest for a ground-nesting raptor in farming habitats. – in review .
- Gillis, H. and Bretagnolle, V. [c]. Is there a balance between physical and social cues for nesting habitat choice in a facultative colonial breeder? – in. prep.
- Goutte, A. 2010. Mécanismes hormonaux impliqués dans la phénologie de la reproduction chez les oiseaux marins polaires. PhD. Thesis, Université de Poitiers, France.
- Greene, C. and Stamps, J. 2001. Habitat selection at low population densities. – *Ecology* 82(8): 2091–2100.
- Gregoire, A., Garnier, S., Dréano, N. and Faivre, B. 2003. Nest predation in Blackbirds (*Turdus merula*) and the influence of nest characteristics. – *Ornis Fennica* 80(1): 1–10.
- Guérif, M., Houles, V., Makowski, D. and Lauvernet, C. 2006. Data assimilation and parameter estimation for precision agriculture using the crop model STICS. – Working with dynamic crop models: evaluation, analysis, parameterization, and applications p. 391.
- Hahn, B. and Silverman, E. 2006. Social cues facilitate habitat selection: American redstarts establish breeding territories in response to song. – *Biology Letters* 2(3): 337.
- Haining, R., Law, J. and Griffith, D. 2009. Modelling small area counts in the presence of overdispersion and spatial autocorrelation. – *Computational Statistics & Data Analysis* 53(8): 2923–2937.
- Hall, L., Krausman, P. and Morrison, M. 1997. The habitat concept and a plea for standard terminology. – *Wildlife Society Bulletin* 25(1): 173–182.
- Hansell, M. 2000. Bird nests and construction behaviour. – Cambridge Univ Pr.
- Hansell, M. and Deeming, D. 2002. Location, structure and function of incubation sites. – *Oxford Ornithology Series* 13: 8–27.
- Helzer, C. and Jelinski, D. 1999. The relative importance of patch area and perimeter-area ratio to grassland breeding birds. – *Ecological Applications* 9(4): 1448–1458.
- Henderson, I., Vickery, J. and Fuller, R. 2000. Summer bird abundance and distribution on set-aside fields on intensive arable farms in southern England.. – *Ecography* 23: 50–59.
- Hendrix, P., Parmelee, R., Crossley, D., Coleman, D., Odum, E. and Groffman, P. 1986. Detritus food webs in conventional and no-tillage agroecosystems. – *Bioscience* 36(6): 374–380.
- Hengl, T., Heuvelink, G. and Stein, A. 2003. Comparison of kriging with external drift and regression-kriging. – Technical note, ITC. Available online at [http://www. itc. nl/library/Academic output](http://www.itc.nl/library/Academic_output) .
- Hobbs, R. 2000. Invasive species in a changing world :Land-use changes and invasions. – Island Press, Washington, DC.



- Holway, D. 1991. Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. – *Condor* pp. 575–581.
- Houghton, J. 1996. *Climate change 1995: the science of climate change.* – vol. 19390. Cambridge Univ Pr.
- Howey, P., Board, R., Davis, D. and Kear, J. 1984. The microclimate of the nests of waterfowl. – *Ibis* 126(1): 16–32.
- Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? – *Trends in Ecology & Evolution* 15(2): 56–61.
- Hurd, C. 1996. Interspecific attraction to the mobbing calls of black-capped chickadees (*Parus atricapillus*). – *Behavioral Ecology and Sociobiology* 38(4): 287–292.
- Hurrell, J. and Trenberth, K. 2010. *Climate Change.* – Oxford University Press.
- Hutchings, J. and Myers, R. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. – *Canadian Journal of Fisheries and Aquatic Sciences* 51(9): 2126–2146.
- Hutto, R. L. 1985. *Habitat selection by nonbreeding, migratory land birds.* – Academic Press, New York.
- Hwang, T., Song, C., Vose, J. and Band, L. 2011. Topography-mediated controls on local vegetation phenology estimated from MODIS vegetation index. – *Landscape ecology* pp. 1–16.
- Hyrenbach, K. and Veit, R. 2003. Ocean warming and seabird communities of the southern California Current System (1987-98): response at multiple temporal scales. – *Deep Sea Research Part II: Topical Studies in Oceanography* 50(14-16): 2537–2565.
- Inman, A. and Krebs, J. 1987. Predation and group living. – *Trends in Ecology & Evolution* 2: 31–32.
- International, B. 2004. *Threatened birds of the world 2004.* – Tech. rep.
- Janzen, F. 1994. Climate change and temperature-dependent sex determination in reptiles. – *Proceedings of the National Academy of Sciences* 91(16): 7487.
- Jenerette, G., Scott, R. and Huete, A. 2010. Functional differences between summer and winter season rain assessed with MODIS derived phenology in a semi arid region. – *Journal of Vegetation Science* 21(1): 16–30.
- Johnson, D. 1980. The comparison of usage and availability measurements for evaluating resource preference. – *Ecology* 61(1): 65–71.
- Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. – *The Auk* 118(2): 557–562.
- Kearney, M. and Porter, W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. – *Ecology Letters* 12(4): 334–350.



- Kerns, C., Ryan, M., Murphy, R., THOMPSON III, F. and Rubin, C. 2010. Factors Affecting Songbird Nest Survival in Northern Mixed Grass Prairie. – *The Journal of Wildlife Management* 74(2): 257–264.
- Kiester, A. 1979. Conspecifics as cues: a mechanism for habitat selection in the Panamanian grass anole (*Anolis auratus*). – *Behavioral Ecology and Sociobiology* 5(4): 323–330.
- Kilner, R. 2006. The evolution of egg colour and patterning in birds. – *Biological Reviews* 81(03): 383–406.
- Kolbe, J. and Janzen, F. 2002. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. – *Ecology* 83(1): 269–281.
- Korpimäki, E. 1992. Fluctuating food abundance determines the lifetime reproductive success of male Tengmalm's owls. – *Journal of Animal Ecology* pp. 103–111.
- Lambeck, R. 1997. Focal species: a multi species umbrella for nature conservation. – *Conservation biology* 11(4): 849–856.
- Lambert, D. 1992. Zero-inflated Poisson regression, with an application to defects in manufacturing. – *Technometrics* pp. 1–14.
- Lambin, X., Bretagnolle, V. and Yoccoz, N. 2006. Vole population cycles in northern and southern Europe: Is there a need for different explanations for single pattern? – *Journal of Animal Ecology* 75(2): 340–349.
- Lauvernet, C. 2005. Assimilation variationnelle d'observations de télédétection dans les modèles de fonctionnement de la végétation: utilisation du modèle adjoint et prise en compte de contraintes spatiales.
- Lawless, J. 1987. Regression methods for Poisson process data. – *Journal of the American Statistical Association* pp. 808–815.
- Lecoustre, V. 2009. Comportement d'approvisionnement d'un prédateur en milieu hétérogène: l'exemple du Busard cendré en paysage agricole. – Master's thesis, Université Pierre et Marie Curie.
- Lehikoinen, E. and Sparks, T. 2010. *Changes in migration*. – Oxford University Press Oxford, UK.
- Lehikoinen, E., Sparks, T. and Zalakevicius, M. 2004. Arrival and departure dates. – *Advances in ecological research* 35: 1–31.
- Levin, S. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. – *Ecology* 73(6): 1943–1967.
- Limiñana, R., Arroyo, B., Surroca, M., Urios, V. and Reig-Ferrer, A. 2011. Influence of habitat on nest location and reproductive output of Montagu's Harriers breeding in natural vegetation. – *Journal of Ornithology* pp. 1–9.
- Limiñana, R., Soutullo, A., Urios, V. and Surroca, M. 2006. Vegetation height selection in Montagu's Harriers *Circus pygargus* breeding in a natural habitat. – *Ardea* 94(2): 280–284.





- Low, M., Arlt, D., Eggers, S. and Pärt, T. 2010. Habitat specific differences in adult survival rates and its links to parental workload and on nest predation. – *Journal of Animal Ecology* 79(1): 214–224.
- Lundberg, S. 1985. The importance of egg hatchability and nest predation in clutch size evolution in altricial birds. – *Oikos* 45(1): 110–117.
- Lusk, J., Wells, K., Guthery, F., Fuhlendorf, S. and Thompson III, F. 2003. Lark sparrow (*Chondestes grammacus*) nest-site selection and success in a mixed-grass prairie. – *The Auk* 120(1): 120–129.
- Magige, F., Moe, B. and Røskaft, E. 2008. The white colour of the Ostrich (*Struthio camelus*) egg is a trade-off between predation and overheating. – *Journal of Ornithology* 149(3): 323–328.
- Major, R. and Kendal, C. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. – *Ibis* 138(2): 298–307.
- Martin, T. 1987. Artificial nest experiments: effects of nest appearance and type of predator. – *Condor* pp. 925–928.
- Martin, T. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. – *Ecological Monographs* 65(1): 101–127.
- Martin, T. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? – *Ecology* 79(2): 656–670.
- Martin, T. 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? – *Ecology* 82(1): 175–188.
- Martin, T. and Roper, J. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. – *Condor* 90(1): 51–57.
- Martin, T., Scott, J. and Menge, C. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. – *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267(1459): 2287.
- Martínez, J., Serrano, D. and Zuberogoitia, I. 2003. Predictive models of habitat preferences for the Eurasian eagle owl *Bubo bubo*: a multiscale approach. – *Ecography* 26(1): 21–28.
- Matson, P., Parton, W., Power, A. and Swift, M. 1997. Agricultural Intensification and Ecosystem Properties. – *Sc* 277: 504–509.
- Mayer, P., Smith, L., Ford, R., Watterson, D., McCutchen, M. and Ryan, M. 2009. Nest construction by a ground-nesting bird represents a potential trade-off between egg crypticity and thermoregulation. – *Oecologia* 159(4): 893–901.
- McCarthy, J. 2001. Climate change 2001: impacts, adaptation, and vulnerability: contribution of Working Group II to the third assessment report of the Intergovernmental Panel on Climate Change. – Cambridge Univ Pr.

- McCarty, J. 2001. Review: Ecological Consequences of Recent Climate Change. – *Conservation Biology* 15: 320–331.
- McGowan, J., Bograd, S., Lynn, R. and Miller, A. 2003. The biological response to the 1977 regime shift in the California Current. – *Deep Sea Research Part II: Topical Studies in Oceanography* 50(14-16): 2567–2582.
- Meijer, T., Daan, S. and Hall, M. 1990. Family planning in the kestrel (*Falco tinnunculus*): the proximate control of covariation of laying date and clutch size. – *Behaviour* pp. 117–136.
- Memmott, J., Craze, P., Waser, N. and Price, M. 2007. Global warming and the disruption of plant–pollinator interactions. – *Ecology Letters* 10: 1–8.
- Merino, S. and Møller, A. 2010. Host–parasite interactions and climate change. – Chapter 15. Oxford University Press.
- Mezquida, E. and Marone, L. 2003. Are results of artificial nest experiments a valid indicator of success of natural nests? – *The Wilson Bulletin* 115(3): 270–276.
- Millon, A. 2006. Influence de la variation cyclique des proies sur un prédateur: approches individuelle et populationnelle du système Busard cendré. Ph.D. thesis, Université Paris 6.
- Millon, A., Arroyo, B. and Bretagnolle, V. 2008. Variable but predictable prey availability affects predator breeding success: natural versus experimental evidence. – *Journal of Zoology* 275(4): 349–358.
- Millon, A., Bourrioux, J., Riols, C. and Bretagnolle, V. 2002. Comparative breeding biology of Hen Harrier and Montagu’s Harrier: an 8-year study in north-eastern France. – *Ibis* 144(1): 94–105.
- Millon, A. and Bretagnolle, V. 2005. Nonlinear and population specific offspring sex ratios in relation to high variation in prey abundance. – *Oikos* 108(3): 535–543.
- Millon, A. and Bretagnolle, V. 2008. Predator population dynamics under a cyclic prey regime: numerical responses, demographic parameters and growth rates. – *Oikos* 117: 1500–1510.
- Møller, A., Fiedler, W. and Berthold, P. 2010. Effects of climate change on birds. – Oxford Univ Pr.
- Montevicchi, W. 1976. Field experiments on the adaptive significance of avian eggshell pigmentation. – *Behaviour* 58(1/2): 26–39.
- Moore, R. and Robinson, W. 2004. Artificial bird nests, external validity, and bias in ecological field studies. – *Ecology* 85(6): 1562–1567.
- Moreno, J. and Osorno, J. 2003. Avian egg colour and sexual selection: does eggshell pigmentation reflect female condition and genetic quality? – *Ecology Letters* 6(9): 803–806.
- Morris, D. W. 2011. Adaptation and habitat selection in the eco-evolutionary process. – *Proceedings of the Royal Society B* 278 (1717): 2401–2411.

- Mougeot, F., Arroyo, B. and Bretagnolle, V. 2001. Decoy presentations as a means to manipulate the risk of extrapair copulation: an experimental study in a semicolonial raptor, the Montagu's harrier (*Circus pygargus*). – Behavioral Ecology 12(1): 1.
- Myneni, R., Keeling, C., Tucker, C., Asrar, G. and Nemani, R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. – Nature 386(6626): 698–702.
- Nordell, S. and Valone, T. 1998. Mate choice copying as public information. – Ecology Letters 1(2): 74–76.
- O'Connor, R. and Shrubbs, M. 1986. Farming and Birds. – Cambridge University Press, Cambridge, UK.
- Orians, G. and Wittenberger, J. 1991. Spatial and temporal scales in habitat selection. – American Naturalist pp. 29–49.
- Parejo, D., White, J., Clobert, J., Dreiss, A. and Danchin, E. 2007. Blue tits use fledgling quantity and quality as public information in breeding site choice. – Ecology 88(9): 2373–2382.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – Annual Review of Ecology, Evolution, and Systematics 37: 637–669.
- Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – Nature 421(6918): 37–42.
- Peach, W., Robinson, R. and Murray, K. 2004. Demographic and environmental causes of the decline of rural Song Thrushes *Turdus philomelos* in lowland Britain. – Ibis 146: S50–S54.
- Pearce-Higgins, J., Yalden, D. and Whittingham, M. 2005. Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae). – Oecologia 143: 470–476.
- Perrins, C. 1977. The role of predation in the evolution of clutch size. – Evolutionary ecology. Macmillan Press, London p. 181–192.
- Perrins, C. and Moss, D. 1975. Reproductive rates in the great tit. – The Journal of Animal Ecology pp. 695–706.
- Peñuelas, J. and Filella, I. 2001. Responses to a warming world. – Science 294(5543): 793.
- Post, E., Stenseth, N., Langvatn, R. and Fromentin, J. 1997. Global climate change and phenotypic variation among red deer cohorts. – Proceedings of the Royal Society of London. Series B: Biological Sciences 264(1386): 1317.
- Potts, G. 1986. The Partridge: Pesticides, Predation and Conservation.. – Collins, London, UK.
- Rettie, W. and Messier, F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. – Ecography 23(4): 466–478.
- Ricklefs, R. and Institution, S. 1969. An analysis of nesting mortality in birds.

- Robinson, R. and Sutherland, W. 2002. Post-war changes in arable farming and biodiversity in Great Britain. – *Journal of Applied Ecology* 39: 157–176.
- Rocamora, G. and Berthelot, D. 1999. Oiseaux menacés et à surveiller en France. Listes rouges et recherche de priorités. Populations. Tendances. Menaces. Conservation.. – Tech. rep., Société d'Etudes Ornithologiques de France/Ligue pour la Protection des Oiseaux, Paris.
- Root, T., Price, J., Hall, K., Schneider, S., Rosenzweig, C. and Pounds, J. 2003. Fingerprints of global warming on wild animals and plants. – *Nature* 421(6918): 57–60.
- Rosenzweig, M. 1991. Habitat selection and population interactions: the search for mechanism. – 137: S5–S28.
- Roy, D. and Sparks, T. 2000. Phenology of British butterflies and climate change. – *Global Change Biology* 6(4): 407–416.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. – *Ecological Applications* 9(1): 135–151.
- Sakamoto, T., Wardlow, B., Gitelson, A., Verma, S., Suyker, A. and Arkebauer, T. 2010. A Two-Step Filtering approach for detecting maize and soybean phenology with time-series MODIS data. – *Remote Sensing of Environment* 114(10): 2146–2159.
- Salamolard, M., Butet, A., Leroux, A. and Bretagnolle, V. 2000. Responses of an avian predator to variations in prey density at a temperate latitude. – *Ecology* 81(9): 2428–2441.
- Schieck, J. and Hannon, S. 1993. Clutch predation, cover, and the overdispersion of nests of the Willow Ptarmigan. – *Ecology* 74(3): 743–750.
- Solis, J. and De Lope, F. 1995. Nest and egg crypsis in the ground-nesting stone curlew *Burhinus oedipnemus*. – *Journal of avian biology* 26(2): 135–138.
- Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K., Tignor, M. and Miller, H. 2007. IPCC, 2007: Climate change 2007: The physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change.
- Sotherton, N. 1998. Land use changes and the decline of farmland wildlife: an appraisal of the set-aside approach. – *Biological Conservation* 83 (3): 259–268.
- Southwood, T. 1977. Habitat, the templet for ecological strategies?. – *Journal of Animal Ecology* 46(2): 337–365.
- Stamps, J. 1988. Conspecific attraction and aggregation in territorial species. – *American Naturalist* pp. 329–347.
- Stenhouse, I., Gilchrist, H. and Montevecchi, W. 2005. Factors affecting nest-site selection of Sabine's Gulls in the eastern Canadian Arctic. – *Canadian Journal of Zoology* 83: 1240–1245.
- Stevens, A., Welch, Z., Darby, P. and Percival, H. 2002. Temperature effects on Florida applesnail activity: implications for snail kite foraging success and distribution. – *Wildlife Society Bulletin* 30 (1): 75–81.



- Stoate, C., Araújo, M. and Borralho, R. 2003. Conservation of european farmland birds: abundance and species diversity. – *Ornis Hungarica* 12-13: 33–40.
- Sugden, L. and Beyersbergen, G. 1986. Effect of density and concealment on American crow predation of simulated duck nests. – *The Journal of Wildlife Management* 50(1): 9–14.
- Sugden, L. and Beyersbergen, G. 1987. Effect of nesting cover density on American crow predation of simulated duck nests. – *The Journal of Wildlife Management* pp. 481–485.
- Sutherland, W. 1996. From individual behaviour to population ecology. – Oxford University Press, USA.
- Thuiller, W. 2003. Impact des changements globaux sur la biodiversité en Europe: projections et incertitudes. Ph.D. thesis. Université Montpellier II, France.
- Tinbergen, N., Impeken, M. and Franck, D. 1967. An experiment on spacing-out as a defence against predation. – *Behaviour* pp. 307–321.
- Travers, M., Clinchy, M., Zanette, L., Boonstra, R. and Williams, T. 2010. Indirect predator effects on clutch size and the cost of egg production. – *Ecology letters* 13(8): 980–988.
- Tscharntke, T., Klein, A., Kruess, A., Steffan-Dewenter, I. and Thies, C. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. – *Ecology letters* 8: 857–874.
- Tucker, G. 1999. Measuring the impacts of agriculture on biodiversity.. – *Environmental Indicators and Agricultural Policy*. – CABI Publishing, Wallingford, U.K.
- Tucker, G. M. and Heath, M. F. 1994. *Birds in Europe: Their Conservation Status*. – Cambridge.
- Tylianakis, J., Didham, R., Bascompte, J. and Wardle, D. 2008. Global change and species interactions in terrestrial ecosystems. – *Ecology letters* 11: 1351–1363.
- Underwood, T. and Sealy, S. 2002. Adaptive significance of egg coloration. – *OXFORD ORNITHOLOGY SERIES* 13: 280–298.
- Valone, T. 2007. From eavesdropping on performance to copying the behavior of others: a review of public information use. – *Behavioral Ecology and Sociobiology* 62(1): 1–14.
- Valone, T. and Templeton, J. 2002. Public information for the assessment of quality: a widespread social phenomenon. – *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 357(1427): 1549.
- Van Bergen, Y., Coolen, I. and Laland, K. 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. – *Proceedings of the Royal Society B: Biological Sciences* 271(1542): 957.
- Velando, A. and Freire, J. 2001. How general is the central-periphery distribution among seabird colonies? Nest spatial pattern in the European Shag. – *The Condor* 103(3): 544–554.



- Visser, M., van Noordwijk, A., Tinbergen, J. and Lessells, C. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). – Proceedings of the Royal Society B 265: 1867–1870.
- Wagner, R. and Danchin, E. 2003. Conspecific copying: a general mechanism of social aggregation. – Animal Behaviour 65(2): 405–408.
- Wall, M., Timmerman-Erskine, M. and Boyd, R. 2003. Conservation impact of climatic variability on pollination of the federally endangered plant, *Clematis socialis* (Ranunculaceae). – Southeastern Naturalist 2(1): 11–24.
- Walsberg, G. 1985. Physiological consequences of microhabitat selection. – PHYSIOL. ECOL. SER. pp. 389–413.
- Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T., Fromentin, J., Hoegh-Guldberg, O. and Bairlein, F. 2002. Ecological responses to recent climate change. – Nature 416(6879): 389–395.
- Wardle, D. 1995. Impact of disturbance on detritus food-webs in agro-ecosystems of contrasting tillage and weed management practices. – Advances in Ecological Research 26: 105–185.
- Weatherhead, P. 2005. Effects of climate variation on timing of nesting, reproductive success, and offspring sex ratios of red-winged blackbirds. – Oecologia 144(1): 168–175.
- Webb, D. 1987. Thermal tolerance of avian embryos: a review. – Condor pp. 874–898.
- Weidinger, K. 2001. Does egg colour affect predation rate on open passerine nests? – Behavioral Ecology and Sociobiology 49(6): 456–464.
- Weidinger, K. and Král, M. 2007. Climatic effects on arrival and laying dates in a long distance migrant, the Collared Flycatcher *Ficedula albicollis*. – Ibis 149(4): 836–847.
- Wells, K. and Fuhlendorf, S. 2005. Comparison of Microclimate at Grassland Bird Nests with Different Substrates. – Prairie Naturalist 37(1): 21.
- Westmoreland, D., Schmitz, M. and Burns, K. 2007. Egg color as an adaptation for thermoregulation. – Journal of Field Ornithology 78(2): 176–183.
- Whittingham, L. and Robertson, R. 1994. Food availability, parental care and male mating success in red-winged blackbirds (*Agelaius phoeniceus*). – Journal of animal ecology pp. 139–150.
- Wiacek, J. 2008. Benefits and costs of semi-colonial breeding in the Montagu's Harrier *Circus pygargus*. – Belg. J. Zool 138(1): 36–40.
- Wiens, J. 1976. Population responses to patchy environments. – Annual Review of Ecology and Systematics 7: 81–120.
- Wiens, J. 1977. On competition and variable environments. – American Scientist .
- Wiens, J. 1989. Spatial scaling in ecology. – Functional ecology 3(4): 385–397.



- Wilson, J., Evans, J., Browne, S. and King, J. 1997. Territory distribution and breeding success of skylarks *Alauda arvensis* on organic and intensive farmland in southern England. – *Journal of Applied Ecology* 34: 1462–1478.
- Wilson, J., Whittingham, M. and Bradbury, R. 2005. The management of crop structure: a general approach to reversing the impacts of agricultural intensification on birds? – *Ibis* 147(3): 453–463.
- Zann, R. 1999. Information constraints in the timing of reproduction in arid-zone birds. – 22nd International Ornithological Congress. Birdlife South Africa, Durban, South Africa. pp. 265–278.
- Zhang, X., Friedl, M., Schaaf, C., Strahler, A., Hodges, J., Gao, F., Reed, B. and Huete, A. 2003. Monitoring vegetation phenology using MODIS. – *Remote sensing of environment* 84(3): 471–475.
- Zuria, I., Gates, J. and Castellanos, I. 2007. Artificial nest predation in hedgerows and scrub forest in a human-dominated landscape of central Mexico. – *Acta Oecologica* 31(2): 158–167.





## CHANGEMENT GLOBAL ET DYNAMIQUE DE SÉLECTION D'HABITAT DE REPRODUCTION D'UN OISEAU NICHANT AU SOL

Comprendre les exigences d'une espèce pour un habitat est une question centrale en conservation et gestion de la biodiversité et elle l'est encore davantage, de nos jours, avec le changement global. Dans ce contexte, ce doctorat vise à étudier la sélection du site de nidification d'une espèce semi-coloniale nichant au sol en milieu agricole, le Busard cendré *Circus pygargus*. Différentes échelles temporelles et spatiales sont utilisées pour comprendre comment les variations environnementales affectent les patrons de sélection de hauteur de végétation au nid, leurs processus et la fitness des individus.

La sélection d'une hauteur de végétation au nid adéquate dépend de deux risques principaux dont l'importance relative change au cours d'une saison de reproduction: le risque de prédation et le risque d'insolation des œufs et poussins. Les busards sélectionnent une hauteur de végétation importante (environ 80cm). Cependant, les variations des trois composantes de l'habitat (phénologie et croissance de la végétation, abondance de proies et présence de congénères) influencent à des degrés divers les patrons de sélection de hauteur de végétation et les paramètres de la reproduction. L'importance du caractère semi-colonial de l'espèce est soulignée : l'attraction conspécifique et la compétition entre couples influencent fortement les patrons de sélection à différentes échelles spatio-temporelles. Une attraction conspécifique s'exerce à large échelle tandis que de la compétition entre couples s'installe à plus petite échelle.

A la lumière de ces éléments, une réflexion quant à l'avenir du busard cendré en milieu agricole intensif dans le contexte du changement global est menée.

*Mots-clés* : sélection d'habitat de reproduction, changement global, milieu agricole, espèce nichant au sol, hauteur de végétation

-----

## GLOBAL CHANGE AND BREEDING HABITAT SELECTION DYNAMICS IN A GROUND-NESTING BIRD

Understanding species habitat requirements is a central issue in biodiversity conservation and management and it is even more important with the actual global change. In this context, we study nest site selection of a semi-colonial ground-nesting species breeding in farmlands, the Montagu's Harrier *Circus pygargus*. We use different spatial and temporal scales to understand how environmental variations affect patterns of vegetation height selection at the nest, their underlying processes and individual fitness.

The selection of an optimal vegetation height at the nest depends on two main risks whose relative importance changes in a breeding season: predation and overheating risks of eggs and chicks. Montagu's Harrier selects tall vegetation at nest (i.e. 80 cm). However, variations of the three components of habitat (vegetation phenology and growth, prey abundance and presence of conspecifics) affect to varying degrees selection patterns of vegetation height and breeding parameters. The importance of the semi-colonial character of the species is further emphasized: conspecific attraction and among-pair competition strongly influence selection patterns at different spatial and temporal scales. Conspecific attraction acts at large scale while among-pair competition appears at finer scale.

In the light of these new elements, we conducted a discussion about the future of Montagu's harrier in intensive agricultural areas in the context of global change.

*Keywords*: breeding habitat selection, global change, agricultural areas, ground-nesting species, vegetation height