

Table des matières

Remerciements	4
Introduction générale.....	9
I. La sélection de l'habitat	10
1. Principe général et définitions	10
2. Les mécanismes impliqués dans la sélection de l'habitat	11
3. Importance de la compétition interspécifique	13
4. Sélection de l'habitat dans les environnements changeants : importance de la plasticité comportementale	14
II. Les systèmes agricoles : des environnements anthropiques fortement dynamiques	17
1. Mutation rapide des systèmes agricoles et déclin de la biodiversité : le cas de l'avifaune	17
2. Effet direct de la perte et de la dégradation des habitats	20
3. Effets indirects via une modification des interactions interspécifiques.....	23
III. La Perdrix grise, une espèce emblématique	24
1. Une espèce à enjeux multiples	24
2. Une espèce en déclin : de la cause initiale aux causes émergentes.....	26
3. Situation actuelle : des populations affaiblies sur des territoires dégradés	28
IV. Objectifs et organisation de la thèse	32
1. Problématique	32
2. Cadre de l'étude.....	33
3. Axes de recherche.....	33
Méthodes générales.....	37
I. Sites d'étude.....	38
II. Protocoles expérimentaux	39
1. Observations ornithologiques.....	39
2. Points d'écoute Perdrix.....	40
3. Suivis GPS de Perdrix grises	41
Chapitre I Changement des patrons de sélection de l'habitat chez la Perdrix grise en relation avec la dynamique du paysage agricole au cours des 20 dernières années	43
<i>Avant-propos et résumé du Chapitre I</i>	44
Abstract	45
Introduction.....	47
Material & methods	49
Results	55
Discussion	59
References.....	63
Supporting information.....	71
Chapitre II Compétition interspécifique entre la Perdrix grise et la Perdrix rouge dans un paysage agricole.....	83
<i>Avant-propos et résumé du Chapitre II</i>	84
Abstract	85
Introduction.....	87

Material & methods	89
Results	94
Discussion	100
References	102
Supporting information	108
Chapitre III Ajustements de la sélection de l'habitat au cours du cycle circadien : une réponse à la spatio-temporalité des perturbations naturelles et humaines ?	115
<i>Avant-propos et résumé du Chapitre III</i>	116
Abstract	117
Introduction	119
Material & methods	121
Results	128
Discussion	134
References	137
Supporting information	147
Chapitre IV Paramètres individuels et ajustements spatiotemporels aux perturbations : quelles perspectives pour la gestion?	155
<i>Avant-propos et résumé du Chapitre IV</i>	156
Abstract	157
Introduction	159
Material & methods	162
Results	165
Discussion	169
References	172
Supporting information	181
Discussion générale	187
I. Dynamique de l'habitat et processus de sélection : la qualité de l'habitat peut-elle être limitante ?	189
II. La compétition interspécifique, une contrainte supplémentaire ?	193
III. Ajustements aux perturbations naturelles et anthropiques : réponses populationnelles et traits individuels	196
IV. Limites et perspectives de recherche	200
V. Implications pour la gestion des populations de Perdrix grise et d'espèces d'intérêt cynégétique	204
1. Améliorer la quantité et la qualité des habitats	205
2. Repenser les « associations » d'espèces lâchées en considérant la compétition interspécifique	206
3. Réduire les sources de perturbation	207
4. Lâcher des oiseaux de qualité	208
5. Comment s'y prendre ? Quels moyens mettre en œuvre ?	210
Références bibliographiques	213
Résumé	242

Introduction générale

I. La sélection de l'habitat

Les animaux vivent et se déplacent dans des environnements hétérogènes (A. R. Johnson, Wiens, Milne, & Crist, 1992; Stewart, John, & Hutchings, 2000; Wiens, 1976). Cette hétérogénéité concerne à la fois les ressources (alimentation, refuges, sites de reproduction, partenaires), ainsi que les menaces auxquelles ils sont confrontés dans leur environnement (prédateurs, compétiteurs, parasites) (voir Sparrow, 1999). Face à cette hétérogénéité, la distribution des organismes est souvent non-aléatoire, résultant de processus de sélection de l'habitat, quasi universels dans le règne animal (Orians & Wittenberger, 1991). Les choix individuels à l'origine de ce processus de sélection ont des répercussions sur la survie et la reproduction des individus (par exemple Alatalo, Lundberg, & Ulfstrand, 1985; Danchin, Boulinier, & Massot, 1998; Gilroy, Anderson, Vickery, Grice, & Sutherland, 2011), ainsi que sur les dynamiques de populations (Bronson, 1979; Donovan & Thompson, 2001; Pulliam & Danielson, 1991). La compréhension du processus de sélection de l'habitat et de sa structuration (spatiale, temporelle) est par conséquent primordiale, reflétant la structuration de potentiels facteurs limitant les populations (Fretwell & Lucas, 1970; Pulliam & Danielson, 1991; Rettie & Messier, 2000).

1. Principe général et définitions

En écologie, l'habitat peut être défini comme un ensemble de facteurs environnementaux physiques et biologiques homogènes, souvent subdivisé en sous-unités ou patchs, qu'une espèce utilise pour survivre et se reproduire (Block & Brennan, 1993; Fretwell & Lucas, 1970; J. Jones, 2001). Plusieurs notions faisant référence au concept d'habitat ont régulièrement été employées dans la littérature de manière ambiguë ou inappropriée (Block & Brennan, 1993; J. Jones, 2001), telles que l'« utilisation de l'habitat » (ou « habitat use » en anglais) et la « sélection de l'habitat » (« habitat selection »). Nous proposons une clarification de ces notions et des mécanismes associés.

L'« utilisation de l'habitat » fait référence à la distribution des individus au sein de chacun des types d'habitat, c'est-à-dire à la quantité de chacun des types d'habitat qu'un individu utilise pour répondre à ses exigences écologiques (Block & Brennan, 1993; Fretwell & Lucas, 1970; D. H. Johnson, 1980; J. Jones, 2001). Elle peut s'exprimer en nombre d'individus, en proportion de la population ou encore en densité d'individus par type d'habitat (Block &

Brennan, 1993; Fretwell & Lucas, 1970; J. Jones, 2001). L'utilisation de l'habitat est souvent confrontée à la disponibilité des différents types d'habitat dans l'environnement (ou « availability »), qui dépend à la fois de leur abondance et de leur accessibilité (D. H. Johnson, 1980).

La « sélection de l'habitat » correspond à l'ensemble des processus comportementaux et environnementaux menant à l'utilisation de l'habitat (Fretwell & Lucas, 1970; D. H. Johnson, 1980; J. Jones, 2001). D. H. Johnson (1980) définit une utilisation sélective de l'habitat comme une utilisation biaisée des différents types d'habitat, par rapport à leur disponibilité. Un habitat est dit préféré ou sélectionné (« preferred », « selected ») lorsqu'il est utilisé dans une proportion supérieure à sa disponibilité, et évité (« avoided ») lorsqu'il est utilisé dans une proportion inférieure à sa disponibilité (D. H. Johnson, 1980).

2. Les mécanismes impliqués dans la sélection de l'habitat

Le processus de sélection de l'habitat repose sur un ensemble de mécanismes comportementaux (par exemple la capacité à identifier un patch d'habitat, le choix de l'utiliser ou non, combien de temps rester dans ce patch, etc.), en réponse à des stimuli environnementaux (disponibilité de la ressource alimentaire, de couverts refuges, présence et distribution des prédateurs, etc.), influençant la survie et la reproduction des individus (Brown, 1988; Fretwell & Lucas, 1970; J. Jones, 2001). Les individus dont le comportement permet d'identifier et de sélectionner les patches d'habitat les plus profitables en termes de survie et de reproduction sont sélectionnés, les individus faisant des choix inadéquats sont contre-sélectionnés (Brown, 1988; Fretwell & Lucas, 1970). Ces choix individuels se basent sur des indices environnementaux reflétant la qualité de l'habitat (« habitat suitability » ; Fretwell & Lucas, 1970), caractérisée par plusieurs facteurs tels que la disponibilité de nourriture, de couverts, ainsi que la présence de prédateurs (Fretwell & Lucas, 1970). Chaque habitat, défini par ses paramètres physiques et biologiques propres, serait donc associé à une valeur habitat-spécifique de survie et de reproduction (Fretwell & Lucas, 1970; T. E. Martin, 1993; Richner, 1989).

La sélection de l'habitat résulte souvent d'un compromis entre le bénéfice tiré de l'utilisation d'un habitat (par exemple le gain énergétique pour les habitats d'alimentation, meilleur succès reproducteur pour le site de reproduction), et la minimisation du risque de prédation (Brown, 1988, 1999; Gilliam & Fraser, 1987; Lima, 2009). Ce mécanisme a

notamment été très étudié dans la sélection du patch d'habitat d'alimentation, dans le cadre de la théorie de l'approvisionnement optimal (Brown, 1988; Charnov, 1976; MacArthur & Pianka, 1966; Rosenzweig, 1981). Par exemple, Butler, Whittingham, Quinn, & Cresswell (2005) montrent que le Pinson des arbres *Fringilla coelebs* L. 1758 sélectionne préférentiellement des habitats d'alimentation à végétation rase, en réponse à un compromis entre gain énergétique et risque de prédation. Lorsque la végétation est courte, le risque de prédation est réduit (meilleure détectabilité des prédateurs). Le Pinson des arbres réduit en conséquence de 13% son comportement anti-prédateur (vigilance), contribuant à augmenter de 13% le temps alloué à l'ingestion, comparé aux habitats à structure de végétation haute (Whittingham, Butler, Quinn, & Cresswell, 2004). Ce rapport coûts/bénéfices est également observé dans la sélection du site de nidification (Lima, 2009; Magana, Alonso, Martin, Bautista, & Martin, 2010; Wiebe & Martin, 1998). Chez certaines espèces nichant au sol, la sélection du site de nidification répondrait à un compromis entre le bénéfice de nidifier dans des couverts végétaux denses favorisant un meilleur succès reproducteur (diminution de la probabilité de prédation des nids), cependant associés à un risque de prédation plus élevé des femelles en incubation (visibilité moindre) (Götmark, Blomqvist, Johansson, & Bergkvist, 1995; Lima, 2009; Magana et al., 2010; Wiebe & Martin, 1998).

La sélection de l'habitat est identifiée comme un processus densité-dépendant (Fretwell & Lucas, 1970; Rosenzweig, 1991; Svärdson, 1949). À faible densité de population, la qualité de l'habitat est maximale (Fretwell & Lucas, 1970). À mesure que la densité de population augmente, la pression imposée par la population (ou compétition intraspécifique ; Rosenzweig, 1991) sur les habitats de qualité augmente, incitant les individus à utiliser des habitats suboptimaux (Fretwell & Lucas, 1970; Rosenzweig, 1991), et favorisant en conséquence l'utilisation d'une plus grande variété d'habitats (Rosenzweig, 1991; Svärdson, 1949). Par exemple, lors de nouvelles colonisations, le Serin des Canaries *Serinus canaria* L. 1758 sélectionne des habitats optimaux pour nidifier, puis étend sa nidification vers des patches suboptimaux lorsque la densité de population augmente (Mayr, 1926; cité par Rosenzweig, 1991; et Svärdson, 1949). Bien que la compétition intraspécifique participe à augmenter la variété des habitats utilisés, phénomène que Rosenzweig (1991) caractérise d'« érosion » de la sélection de l'habitat, la compétition interspécifique participe quant à elle à la contraindre (MacArthur & Levins, 1964; Rosenzweig, 1991; Svärdson, 1949).

3. Importance de la compétition interspécifique

La compétition interspécifique est l'un des déterminants majeurs des interactions trophiques, des niches écologiques, des patrons biogéographiques, et plus généralement des processus adaptatifs (Bull, 1991; Gause, 1934; Grand & Dill, 1999; MacArthur & Levins, 1964; Svårdson, 1949). C'est également l'un des principaux déterminants du processus de sélection de l'habitat, particulièrement entre espèces phylogénétiquement et écologiquement proches (c'est-à-dire en termes d'exigences écologiques : préférences d'habitat, régime alimentaire, phénologie de reproduction, etc.) (Brown, 1988; Grand & Dill, 1999; MacArthur & Levins, 1964; Rosenzweig, 1981; Svårdson, 1949). La compétition interspécifique peut prendre la forme d'une compétition indirecte par exploitation (ou déplétion) de la ressource. Les individus sont alors libres d'accéder à la ressource, mais l'utilisation de cette ressource par certains individus en limite l'abondance pour les autres (Dhondt, 2012; Schoener, 1983; Wiens, 1992). La compétition par interférence implique quant à elle des interactions interspécifiques directes, souvent agressives (ou agonistiques) visant à empêcher l'accès d'un individu à une ressource (Dhondt, 2012; Wiens, 1992). Dans les deux cas, la disponibilité de la ressource est altérée pour au moins l'une des espèces impliquées (limitation de l'abondance dans une compétition par exploitation, de l'accessibilité dans une compétition par interférence), pouvant affecter ses paramètres démographiques (Dhondt, 2012; Högstedt, 1980; P. R. Martin, Freshwater, & Ghahambor, 2017; P. R. Martin & Martin, 2001b).

Les interactions de compétition interspécifique sont coûteuses (augmentation du temps et de l'énergie alloués à l'acquisition de la ressource qui se raréfie, coûts énergétiques directs des comportements agonistiques et indirects des opportunités manquées d'acquisition de la ressource ; Gill, 1978; Maurer, 1984; Wiens, 1992). L'évolution tend à minimiser ces interactions par des processus de différenciation écologique (Hardin, 1960; MacArthur & Levins, 1964), tels que la différenciation de la sélection de la ressource entre espèces phylogénétiquement proches, que ce soit à des échelles larges (ségrégation des aires de répartition), ou à échelle locale (différenciation des micro-habitats utilisés, du régime alimentaire) (Lawlor & Smith, 1976; MacArthur & Levins, 1964; Rosenzweig, 1991; Svårdson, 1949). Cette ségrégation est souvent maintenue par des comportements agonistiques, tels que le chant par exemple chez les oiseaux (Jankowski, Robinson, & Levey, 2010; P. R. Martin & Martin, 2001a; McEntee, 2014). Jankowski et al. (2010) mettent notamment en évidence un maintien des distributions altitudinales de deux espèces d'oiseaux tropicaux assuré par

l'augmentation des comportements agonistiques interspécifiques à proximité de la zone de contact entre leurs distributions respectives.

La compétition interspécifique entre espèces phylogénétiquement et écologiquement proches a par ailleurs été bien étudiée chez de nombreuses espèces d'oiseaux et implique souvent des conséquences asymétriques pour les espèces impliquées (P. R. Martin et al., 2017; Persson, 1985; Schoener, 1983; Wiens, 1992). Dans P. R. Martin et al. (2017), 224 sur 270 (soit 83,0%) paires d'espèces d'oiseaux phylogénétiquement proches sont impliquées dans une relation de compétition par interférence dont les conséquences sont asymétriques, et bénéficient à l'espèce la plus grosse dans 87% des cas (coût moins élevé pour l'espèce la plus grosse de s'engager dans une interférence avec un compétiteur plus petit que l'inverse, voir Persson, 1985; Schoener, 1983). Dans ce type de compétition, la dynamique de population de l'espèce dominée (ou subordonnée) peut être particulièrement affectée par la diminution de l'accès à la ressource, affectant son succès reproducteur. Par exemple, en présence de la Paruline verdâtre *Leiothlypis celata* S. 1822, espèce dominante, la Paruline de Virginia *Leiothlypis virginiae* B. 1860, espèce dominée, modifie la sélection de son site de nidification vers des habitats de moins bonne qualité (P. R. Martin & Martin, 2001b). Le succès reproducteur de l'espèce dominée est affecté (le nombre de jeunes à l'envol augmente de 1,4 à 2,3 juvéniles/nid lors de la suppression expérimentale de l'espèce dominante ; P. R. Martin & Martin, 2001a), à la fois par un moins bon accès à la ressource alimentaire (augmentation de 95% des taux d'alimentation en période d'incubation et 43% de l'alimentation des juvéniles par les parents lors de la suppression expérimentale de l'espèce dominante ; P. R. Martin & Martin, 2001a), ainsi que par un taux de prédation des nids plus fort (supérieur de 52%) en situation de co-occurrence des deux espèces (P. R. Martin & Martin, 2001a). La compétition interspécifique joue donc un rôle déterminant dans le processus de sélection de l'habitat et d'accès à la ressource, affectant en conséquence les dynamiques de populations des espèces impliquées.

4. Sélection de l'habitat dans les environnements changeants : importance de la plasticité comportementale

Influencé par la disponibilité de l'habitat, le risque de prédation et la compétition interspécifique, le processus de sélection de l'habitat devrait être affecté par les variations de ces paramètres, susceptibles d'affecter en conséquence les dynamiques de populations.

Dans les environnements fortement dynamiques tels que les milieux anthropisés, les changements environnementaux soudains de l'habitat (disponibilité et distribution des ressources, modifications des interactions interspécifiques) peuvent créer un décalage ou une rupture entre les choix adaptatifs de sélection d'un habitat, et la qualité actuelle, qui n'est plus corrélée à la qualité originellement offerte par cet habitat (B. A. Robertson, Rehage, & Sih, 2013; Schlaepfer, Runge, & Sherman, 2002). En d'autres termes, les individus préfèrent des habitats associés à une moins bonne survie ou un moins bon succès reproducteur, ou évitent des habitats pourtant de bonne qualité (Gilroy & Sutherland, 2007; B. A. Robertson et al., 2013; Schlaepfer et al., 2002). Par exemple, dans les milieux agricoles, la Bergeronnette printanière *Motacilla flava* L. 1758 et l'Alouette des champs *Alauda arvensis* L. 1758 sélectionnent préférentiellement leur site de nidification à proximité des passages de roues de tracteurs dans les champs de céréales (le couvert végétal moins dense favoriserait un meilleur accès au sol pour nidifier), bien que leur succès reproducteur soit réduit en raison d'un taux de prédation plus élevé (Gilroy et al., 2011; Gilroy & Sutherland, 2007).

La plasticité phénotypique joue un rôle crucial dans la réponse des populations aux changements environnementaux rapides induits par l'homme (« Human-Induced Rapid Environmental Changes » ou « HIREC »; Sih, Ferrari, & Harris, 2011), et dans l'évolution future des comportements et réponses adaptatives (Hendry, Farrugia, & Kinnison, 2008; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Sih et al., 2011). Sih et al. (2011) soulignent l'importance d'étudier la plasticité comportementale afin d'évaluer si les ajustements observés sont adéquats et suffisants pour faire face aux changements environnementaux (des ajustements inadéquats pouvant mener à des déclinis substantiels des populations ; Sih et al., 2011). À partir de l'étude de 3000 taux de changements phénotypiques recensés dans différents taxons (principalement oiseaux, mammifères, poissons, arthropodes), Hendry et al. (2008) relèvent 1,7 fois plus de changements phénotypiques en milieux anthropiques qu'en milieux naturels. Ces changements phénotypiques, particulièrement brutaux lorsqu'engendrés par une perturbation anthropique, résulteraient majoritairement de plasticité phénotypique plutôt que d'adaptations génétiques. Un exemple d'ajustement comportemental suite à une modification soudaine de la structuration spatiotemporelle du risque (augmentation du dérangement humain) est mis en évidence par Pan et al. (2011). Ces auteurs montrent, chez une population de Cerf d'Eld *Rucervus eldii* M. 1842 réintroduite dans un milieu à forte activité humaine, une modification des patrons d'activité, comparé à la population source (localisée

en réserve, non soumise au dérangement humain), vers une augmentation de l'activité nocturne asynchrone avec l'activité humaine (voir aussi Gaynor, Hojnowski, Carter, & Brashares, 2018; Lone, Loe, Meisingset, Stamnes, & Myrseth, 2015; Norum et al., 2015). Le dérangement humain modifie donc la structuration spatiotemporelle du risque et devrait être considéré comme partie intégrante du risque de prédation (voir Ciuti et al., 2012; Frid & Dill, 2002). Cet exemple révèle l'importance de la plasticité comportementale face aux variations spatiotemporelles des perturbations environnementales (risque de prédation induit par des prédateurs naturels ou par les activités humaines ; Ciuti et al., 2012; Frid & Dill, 2002), et de sa prise en compte en conservation et gestion des populations.

En gestion et conservation des populations soumises aux changements anthropiques rapides, l'intérêt de considérer les causes locales d'ajustement des patrons de sélection de l'habitat est de plus en plus recommandé (López-Jamar, Casas, Díaz, & Morales, 2011; B. A. Robertson et al., 2013; Schlaepfer et al., 2002). López-Jamar et al. (2011) défendent cette idée à partir d'une étude synchronique de deux populations de Grande Outarde *Otis tarda* L. 1758 à échelle locale. Ils mettent en évidence une différence de patrons de sélection de l'habitat, en réponse à un changement d'occupation du sol dans les milieux agricoles (création d'infrastructures aéroportuaire). Cependant, à ce jour, les études considérant ces ajustements restent rares, et particulièrement les études diachroniques mettant en lumière les mécanismes fins d'ajustement temporel des patrons de sélection de l'habitat en relation avec la dynamique environnementale.

La diversité comportementale (ou diversité interindividuelle des types comportementaux) des populations serait également primordiale dans la réponse et la résilience des populations aux pressions environnementales (Arroyo, Mougeot, & Bretagnolle, 2017; T. Caro & Sherman, 2012; Sih et al., 2012; Sih & Del Giudice, 2012). En effet, les différents types comportementaux ne performant pas de la même manière en fonction du changement environnemental subi (López & Martín, 2015) : comparés aux individus timides (« shy »), les individus téméraires (« bold ») explorent un nouvel environnement plus rapidement (« fast-explorers ») (Cockrem, 2007; Sih & Del Giudice, 2012; Verbeek, Drent, & Wiepkema, 1994), réutilisent un habitat plus rapidement après un dérangement (van Oers, de Jong, Drent, & van Noordwijk, 2004; van Oers, Drent, Goede, & Noordwijk, 2004), mais ont en revanche une moins bonne capacité d'ajustement aux changements environnementaux (Quinn & Cresswell, 2005; Sih & Del Giudice, 2012; Verbeek et al., 1994), et font face à un

risque de mortalité plus élevé (Smith & Blumstein, 2008; van Oers, de Jong, et al., 2004). Holtmann, Santos, Lara, & Nakagawa (2017) mettent en évidence une sélection de l'habitat différenciée selon la personnalité des individus chez l'Accenteur mouchet *Prunella modularis* L. 1758, en réponse au dérangement humain (voir aussi Bonnot et al., 2014). Les individus les plus téméraires s'installent dans des zones à forte perturbation anthropique, et leur témérité augmente avec l'âge. Les individus téméraires pourraient donc être plus aptes à répondre adéquatement aux changements anthropiques. Arroyo et al. (2017) démontrent par exemple chez le Busard cendré *Circus pygargus* L. 1758 en situation de fort dérangement anthropique, un meilleur succès reproducteur (perte de couvée moindre et meilleur nombre de jeunes à l'envol) chez les individus téméraires, ayant contribué à l'augmentation de la témérité au niveau populationnel au cours du temps. Cependant, la variabilité comportementale interindividuelle (ou diversité comportementale au niveau populationnel) reste rarement considérée en conservation et gestion des populations (voir T. Caro & Sherman, 2012), bien qu'elle influencerait les réponses aux changements anthropiques rapides (fragmentation de l'habitat, chasse, autres dérangements humains ; McDougall, Réale, Sol, & Reader, 2006).

Dans les milieux anthropisés où les dynamiques environnementales sont accélérées, il apparaît donc que l'étude des variations de pressions environnementales auxquelles les populations sont exposées (disponibilité de l'habitat, compétition, risque de prédation induit par des prédateurs naturels ou par les activités humaines, voir Ciuti et al., 2012; Frid & Dill, 2002), ainsi que leur réponse comportementale (aux niveaux populationnel et individuel) soient primordiales pour évaluer la capacité des populations à faire face aux changements environnementaux (Sih et al., 2011).

II. Les systèmes agricoles : des environnements anthropiques fortement dynamiques

1. Mutation rapide des systèmes agricoles et déclin de la biodiversité : le cas de l'avifaune

La modification de 50% de la couverture terrestre figure parmi les changements environnementaux rapides induits par l'homme (McGill, Dornelas, Gotelli, & Magurran, 2015; Sih et al., 2011). Les systèmes agricoles représentent l'un des biomes terrestres les plus étendus (40% de la surface émergée du globe; Foley et al., 2005), dans lesquels

l'intensification de l'agriculture illustre particulièrement bien cette transformation anthropique rapide (voir Encart 1), identifiée comme l'une des principales causes de destruction et de fragmentation des habitats (Sih et al., 2011; Wilcove, Rothstein, Dubow, Phillips, & Losos, 1998).

Encart 1 La mutation des systèmes agricoles : de l'expansion à l'intensification

La mutation des systèmes agricoles survient en réponse à l'augmentation des besoins alimentaires induits par la croissance de la population humaine (de 600 millions à 7,2 milliards d'habitants entre 1700 et 2014, Fig. 1a ; Gerland et al., 2014; Piketty, 2013), ainsi qu'à la désertion de la main d'œuvre dans les zones rurales au profit des villes (Griffon, 2006). Deux processus se succèdent : l'expansion de l'utilisation des terres et l'intensification de la production agricole (Matson, Parton, Power, & Swift, 1997; Meyer & Turner, 1992; Naylor, 1996). Entre 1700 et 1980, pour répondre à une augmentation quasi-linéaire de la population humaine (Fig. 1a ; Piketty, 2013), l'expansion de l'agriculture (conversion de terres non cultivées en terres cultivées) est quantifiée à 466% de gain de terres cultivées à l'échelle planétaire (Meyer & Turner, 1992).

À partir des années 1950, la population humaine croît de manière exponentielle (de 2,5 à 7,2 milliards entre 1950 et 2014, Fig. 1a ; Gerland et al., 2014; Piketty, 2013) alors que la main d'œuvre diminue (désertion des zones agricoles au profit des villes dans la période d'après-guerre ; Griffon, 2006). En Europe, dès 1957, la Communauté économique européenne porte et organise un plan de modernisation de l'agriculture (la Politique Agricole Commune, entrée en vigueur à partir de 1962), visant à accroître l'efficacité de production par le progrès technique (Grant, 1997). Le machinisme agricole, l'utilisation de produits sanitaires et fertilisants issus de l'industrie agrochimique, la sélection variétale et l'irrigation se développent et se généralisent (Foley et al., 2005; Grant, 1997; Matson et al., 1997). Les rendements augmentent considérablement entre les années 1960 et 1990, par exemple multipliés par 2 pour les céréales à l'échelle mondiale (Foley et al., 2005; Naylor, 1996), et plus que triplés pour le blé en France (Fig. 1b), au détriment de l'hétérogénéité des habitats (Benton, Vickery, & Wilson, 2003), et de la biodiversité des milieux agricoles (Donald, Green, & Heath, 2001; Maxwell, Fuller, Brooks, & Watson, 2016; Robinson & Sutherland, 2002; Sotherton & Self, 2000).

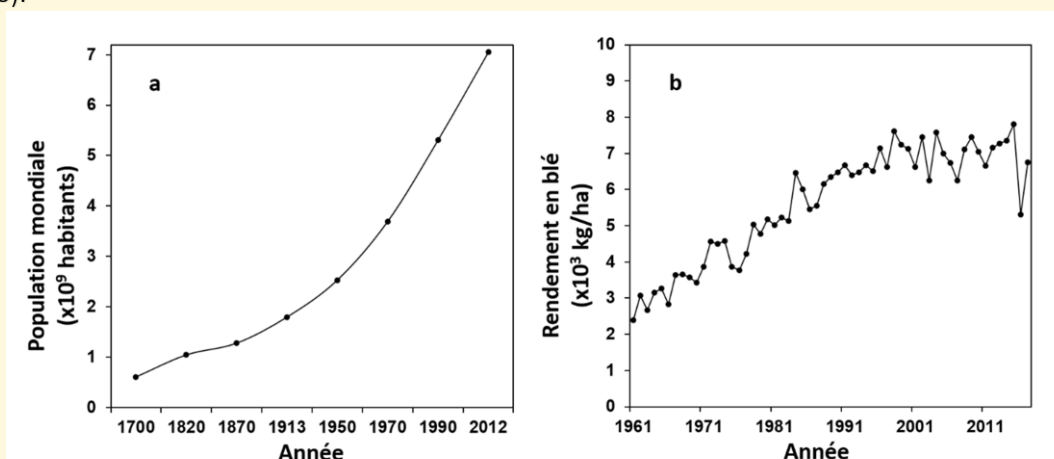


Figure 1 Dynamique de croissance de la population humaine mondiale entre 1700 et 2012 (a ; Piketty, 2013) ; et dynamique des rendements en céréales en France entre 1961 et 2017 (b ; FAO, 2019).

En 2016, une étude mondiale identifie les activités agricoles comme la 2^{nde} menace pesant sur la biodiversité à l'échelle planétaire, juste après la surexploitation (Maxwell et al., 2016). 62% des 8688 espèces menacées ou quasi-menacées d'extinction étudiées vivent en milieux agricoles et ont été affectées par l'expansion et/ou l'intensification de l'agriculture (Maxwell et al., 2016). Dans ces milieux, les déclin d'espèces ont été documentés pour l'ensemble des taxons (e.g. mammifères : Robinson & Sutherland, 2002; oiseaux : Donald et al., 2001; R. J. Fuller et al., 1995; Krebs, Wilson, Bradbury, & Siriwardena, 1999; amphibiens : Robinson & Sutherland, 2002; reptiles : Ribeiro, Santos, Sillero, Carretero, & Llorente, 2009; Robinson & Sutherland, 2002; arthropodes : Sotherton & Self, 2000, espèces végétales : 2000).

Cependant, la situation des oiseaux a été identifiée comme particulièrement préoccupante (Benton et al., 2003; Robinson & Sutherland, 2002). L'effondrement des populations d'oiseaux nicheurs en milieux agricoles a été documenté à plusieurs reprises (Chamberlain, Fuller, Bunce, Duckworth, & Shrubbs, 2000; Donald et al., 2001; Inger et al., 2015; Krebs et al., 1999; Robinson & Sutherland, 2002), estimé par exemple à quatre cinquièmes des espèces en déclin parmi l'ensemble des oiseaux nichant dans les milieux agricoles en Grande-Bretagne (Robinson & Sutherland, 2002). L'abondance des oiseaux spécialistes des milieux agricoles a chuté de 32%, entre 1990 et 2015 à l'échelle de l'Europe (Fig. 2a), et de 52% entre 1989 et 2017 à l'échelle de la France (Fig. 2b).

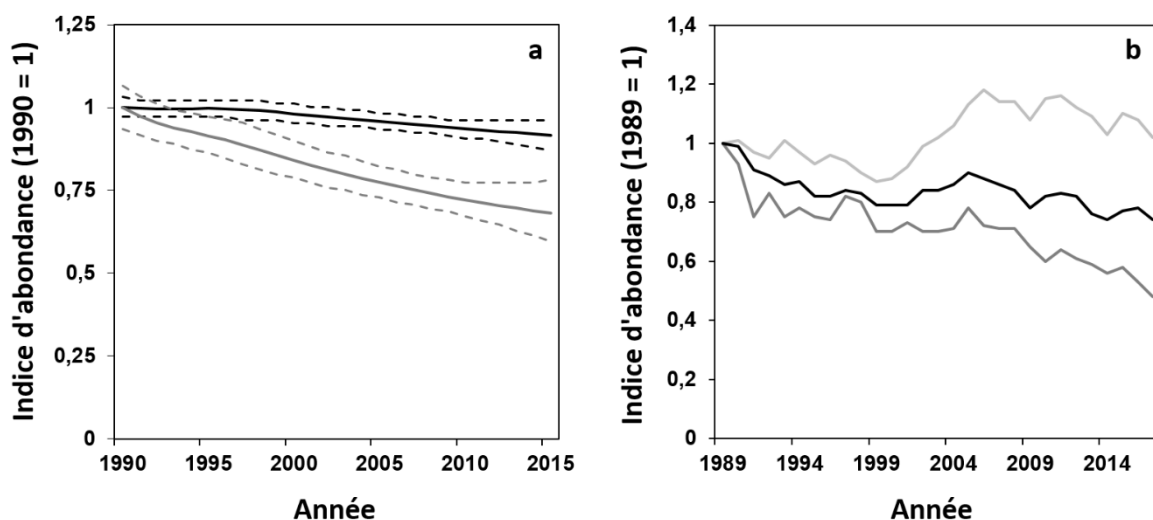


Figure 2 Tendances de l'indice d'abondance des oiseaux communs en Europe (a, 1990-2015), et en France (b, 1989-2017). Les courbes noires font référence à l'ensemble des espèces (168 espèces pour l'Europe, 75 pour la France), les courbes gris foncé représentent les espèces spécialistes des milieux agricoles (38 en Europe, 24 en France), et la courbe gris clair correspond aux espèces généralistes en France (14 espèces). Sources: EBCC (2019); Vigie-Nature (2018).

Par leur position dans le réseau trophique, les oiseaux représentent un groupe sentinelle de l'état des agrosystèmes (Gregory, Noble, & Custance, 2004; Whittingham et al., 2009). Leur déclin est particulièrement préoccupant car il pourrait refléter des tendances similaires concomitantes au sein du réseau trophique (voir Gregory et al., 2004), et notamment un déclin d'adventices et de graines (Fried, Petit, Dessaint, & Reboud, 2009; Robinson & Sutherland, 2002), ou d'arthropodes (Robinson & Sutherland, 2002), menaçant en conséquences les fonctions associées au maintien de l'agriculture. Au Royaume-Uni, 19 espèces d'oiseaux spécialistes des milieux agricoles sont utilisées en tant qu'espèces indicatrices dans le « Farmland Bird Indicator » (ou littéralement « indicateur oiseaux des milieux agricoles »), un indice de la qualité de vie de la biodiversité dans les milieux agricoles (Aebischer et al., 2003; Ormerod & Watkinson, 2000; Sotherton, Aebischer, & Ewald, 2014). Sur ces 19 espèces, 12 ont décliné entre 1970 et 2007 au Royaume-Uni (-27 à -94% de déclin ; RSPB, 2019), 16 ont décliné en France entre 1989 et 2018 (-18% à -62% ; Vigie-Nature, 2018). Dans leur article « Farmland biodiversity : is habitat heterogeneity the key ? », Benton et al. (2003) identifient la diminution de quantité et de qualité des habitats et des ressources alimentaires comme principaux facteurs ayant affecté les paramètres démographiques des populations d'oiseaux.

2. Effet direct de la perte et de la dégradation des habitats

L'intensification de l'agriculture est maintenant identifiée et reconnue comme première cause de déclin des oiseaux vivant en milieux agricoles (Chamberlain et al., 2000; Donald et al., 2001; Robinson & Sutherland, 2002). Le déclin et la contraction des aires de distribution, accrus dans les pays où l'agriculture est plus intensive (pays membres de l'Union Européenne avant 1990, principalement en Europe de l'Ouest), soutiennent par ailleurs cette idée (Báldi & Faragó, 2007; Donald et al., 2001; Donald, Pisano, Rayment, & Pain, 2002).

Benton et al. (2003) synthétisent les effets en cascade menant de l'intensification des pratiques agricoles au déclin des populations d'oiseaux : la modification des pratiques (gestion des habitats non cultivés, types de cultures, densité des semis, calendriers culturaux, utilisation de fertilisants, de pesticides, évolution des itinéraires techniques) ont directement affecté l'hétérogénéité des habitats dans les paysages agricoles (Encart 2). La perte engendrée de diversité, d'abondance et de qualité des habitats (habitats de nidification, d'alimentation, refuges) et de la ressource alimentaire (insectes, graines) a affecté les paramètres

démographiques (survie, succès reproducteur), ainsi que les dynamiques de populations (Benton, Bryant, Cole, & Crick, 2002; Benton et al., 2003; Potts & Aebischer, 1991).

L'abondance de graines, associée à la distribution des oiseaux granivores (Moorcroft, Whittingham, Bradbury, & Wilson, 2002), a considérablement diminué dans les milieux agricoles (-42% en richesse spécifique et -67% en densité d'adventices entre 1970 et 2005 en Bourgogne, France dans Fried et al., 2009; voir aussi Robinson & Sutherland, 2002). Cette diminution est préoccupante pour le maintien des populations d'oiseaux, tels que l'Alouette des champs dont les besoins alimentaires quotidiens sont estimés à 8 grammes de graines (soit 4200 à 5600 graines) par individu et par jour (Eraud et al., 2015), ou le Bruant jaune *Emberiza citrinella* L. 1758 et la Perdrix grise *Perdix perdix* L. 1758 qui se nourrissent rarement en automne dans les champs où la densité de graines est inférieure à 50 graines/m² (Moorcroft et al., 2002). L'abondance et la diversité d'insectes ont également été affectées par l'intensification de l'agriculture, à la fois par la suppression des habitats semi-naturels et l'utilisation de pesticides (Brickle, Harper, Aebischer, & Cockayne, 2000; Kovács-Hostyánszki, Kőrösi, Orci, Batáry, & Báldi, 2011; Sánchez-Bayo & Wyckhuys, 2019). Par exemple, la richesse spécifique d'espèces végétales, d'Orthoptères et de Lépidoptères diminue avec l'augmentation du degré d'intervention dans les parcelles agricoles (le long d'un gradient prairie permanente – jachères – culture annuelle type céréales ; Kovács-Hostyánszki et al., 2011). Cette disponibilité d'insectes affecte la dynamique des populations d'oiseaux, aussi bien insectivores que granivores (Benton et al., 2002; Potts & Aebischer, 1991; Wilson, Morris, Arroyo, Clark, & Bradbury, 1999). Par exemple, le succès reproducteur de la Perdrix grise, espèce granivore, est affecté par la diminution de l'abondance d'insectes (Potts & Aebischer, 1991), les juvéniles étant strictement insectivores pendant les premiers jours suivant l'éclosion car physiologiquement incapables de digérer des graines (Green, Rands, & Moreby, 1987).

Brickle et al. (2000) mettent également en évidence une masse corporelle supérieure chez des juvéniles de Bruant proyer *Emberiza calandra* L. 1758 lorsque la densité d'insectes dans un rayon de 115 mètres autour du nid est élevée, et que le temps alloué à la recherche alimentaire par les parents est, en conséquence, réduit. La sélection de l'habitat et du site de nidification est donc cruciale pour assurer un bon succès reproducteur. Cependant, à ce jour, les mécanismes d'ajustement temporel de la sélection de l'habitat en réponse à la dynamique des habitats dans les paysages agricoles soumis à l'intensification, restent méconnus.

Encart 2 Concept de paysage et d'hétérogénéité paysagère appliqués aux agrosystèmes

Le paysage est défini comme une unité écologique intermédiaire (entre échelle locale et régionale), caractérisée par une mosaïque de patchs d'habitats, suffisamment large (de l'ordre du km²) pour contenir un motif répété dans les composantes ou écosystèmes (Dunning, Danielson, & Pulliam, 1992; Forman & Godron, 1981). Cette échelle intermédiaire permet notamment de faire le lien entre l'échelle locale (c'est-à-dire l'échelle de l'habitat) et les échelles plus larges, de l'ordre de grandeur de l'aire de distribution de l'espèce étudiée, et d'analyser les processus écologiques intervenant à l'interface entre ces deux échelles (Dunning et al., 1992). Par la présence de différents patchs d'habitats, les paysages sont souvent très hétérogènes, ce qui leur confère la capacité de soutenir de nombreuses espèces (Forman & Godron, 1981; Tews et al., 2004).

L'hétérogénéité spatiale des paysages est caractérisée par une composante compositionnelle (nature et proportion des différents éléments paysagers) et une composante configurationnelle (forme et arrangement spatial de ces éléments dans le paysage) (Dunning et al., 1992; Forman & Godron, 1981). Ces deux composantes ont été affectées par l'intensification de l'agriculture, créant des unités de plus en plus grandes sous le même type de gestion agricole à un moment donné (Fig. 3). La spécialisation des exploitations (diminution des zones d'agriculture diversifiées à l'échelle régionale tels que les systèmes mixtes de polyculture élevage ; Benton et al., 2003; Stoate et al., 2009) et la simplification des pratiques (diminution de la diversité des cultures et variétés cultivées ; Benton et al., 2003; Matson et al., 1997) ont réduit l'hétérogénéité compositionnelle. L'agglomération des exploitations, l'augmentation de la taille des parcelles (et donc de la distance entre les patchs d'habitats), la destruction d'éléments semi-naturels (bandes enherbées, haies, habitats non cultivés tels que les étangs, ronciers, friches, etc.) ont affecté l'hétérogénéité configurationnelle (Benton et al., 2003).

Dans les paysages agricoles, Vasseur et al. (2013) distinguent une composante moins étudiée de l'hétérogénéité, qu'ils nomment hétérogénéité « cachée » (ou « hidden heterogeneity »), correspondant à l'hétérogénéité spatiotemporelle engendrée par la dynamique temporelle rapide des paysages (par exemple les successions de cultures). Cette composante a été affectée par la simplification des rotations culturales et le remplacement de variétés de printemps par des variétés d'hiver (Benton et al. 2003; Newton, 2004). La faible variation interannuelle des cultures plantées, associée à la réduction de la pratique de maintien de chaumes et d'intercultures, de couverts refuges et d'alimentation (graines, insectes) pour les oiseaux (Newton, 2004), ont mené à une homogénéisation spatiotemporelle des paysages.



Figure 3 Photographies aériennes d'un paysage agricole (même emprise spatiale) à deux dates différentes (1958, 2014) localisé sur la commune Les Fosses, Zone Atelier « Plaine & Val de Sèvre », Deux-Sèvres, France.

Source : © IGN (2019).

3. Effets indirects via une modification des interactions interspécifiques

Dans une phase plus avancée de l'intensification de l'agriculture, les habitats sont dégradés et fragmentés (Benton et al., 2003; Donald et al., 2001; Lindenmayer & Fischer, 2013; Stoate et al., 2001). La perte et la fragmentation des habitats a indirectement engendré l'émergence de nouvelles menaces par la modification des interactions interspécifiques (Sih et al., 2011) : l'augmentation de la pression de compétition et de prédation dans les habitats restants (Dhondt, 2012; Newton, 2004; Pasitschniak-Arts & Messier, 1995; Robillard, Garant, & Bélisle, 2013; Schlaepfer et al., 2002).

Devant la diminution de la quantité et de la qualité des habitats et des ressources alimentaires, une augmentation de la pression de compétition dans les patchs d'habitats favorables restants est attendue entre espèces partageant des exigences écologiques proches (site de nidification, régime alimentaire des adultes, des juvéniles, etc.). Cette question reste étonnamment peu documentée. Newton (2004) relevait d'ailleurs que l'augmentation de la pression de compétition avait rarement été suggérée comme facteur de déclin des oiseaux dans les milieux agricoles, et gagnerait à être considérée comme facteur additionnel. Robillard et al. (2013) publient l'une des premières études suggérant une pression de compétition interspécifique accrue suite à la perte d'habitat (cavités pour nidifier) induite par l'intensification de l'agriculture. Leurs résultats montrent qu'en l'absence de Moineau domestique *Passer domesticus* L. 1758, l'occupation de nichoirs artificiels par l'Hirondelle bicolore *Tachycineta bicolor* V. 1808 est de 90%, et chute à 20% lorsque la densité de Moineau domestique est élevée. Ils montrent également que l'occupation des nichoirs par l'Hirondelle bicolore a diminué de 19% dans le même temps que l'occupation par le Moineau domestique a augmenté de 12,5%. Cependant, bien que le choix de l'habitat de nidification soit déterminant pour la survie et la reproduction (Brickle et al., 2000; Lima, 2009; T. E. Martin, 1993), les mécanismes fins impliqués dans la modification des patrons de sélection de l'habitat de reproduction en réponse à la compétition interspécifique, restent à ce jour peu documentés chez les oiseaux des milieux agricoles.

La perte d'abondance et de qualité des habitats (notamment des habitats semi-naturels ayant une fonction de refuge : prairies permanentes, friches, haies, bandes enherbées, habitats non cultivées) ont également pu contribuer à concentrer les proies et prédateurs dans les habitats favorables restants, augmentant en conséquence la pression de prédation (Bro, Mayot, Corda, & Reitz, 2004; Pasitschniak-Arts & Messier, 1995; B. A. Robertson et al.,

2013; Weldon & Haddad, 2005). Bro et al. (2004) montrent par exemple que la création de bandes refuges sous forme de patchs isolés, de petite taille, pourrait s'avérer contre-productive pour la gestion de la faune sauvage. Ces patchs concentreraient les proies et prédateurs, n'améliorant pas le succès reproducteur de l'espèce Perdrix grise, voire même augmenteraient les taux de prédateurs hivernaux (Bro et al., 2004). Aebischer & Ewald (2012) identifient même l'augmentation de la pression de prédation dans les derniers habitats favorables (associé à l'augmentation de l'abondance de prédateurs) parmi les trois principales causes de déclin de la Perdrix grise au Royaume-Uni. Les modifications des interactions prédateurs-proies, auxquelles s'additionne le dérangement induit par les activités humaines (dont les effets sont comparables au risque de prédation ; Ciuti et al., 2012; Frid & Dill, 2002; Tolon et al., 2009) dans ces milieux anthropisés (activité agricole, activité cynégétique), devraient également altérer le risque de prédation des espèces proies, leur accès à l'habitat, et par conséquent, façonner leurs patrons de sélection de l'habitat.

III. *La Perdrix grise, une espèce emblématique*

1. *Une espèce à enjeux multiples*

La Perdrix grise *Perdix perdix* L. 1758 (Galliformes, *Phasianidae*) est une espèce d'oiseau emblématique et patrimoniale des milieux agricoles (Bro, 2016). Elle représentait l'une des espèces d'oiseaux les plus communes dans les milieux agricoles, et représente une espèce traditionnelle d'oiseau gibier en Europe (Aebischer & Ewald, 2010, 2012; Buner, Browne, & Aebischer, 2011), la plus populaire et la plus appréciée de Grande-Bretagne et de France (Aebischer, 1997; Bro, Arroyo, & Migot, 2006), ainsi que la quatrième espèce de petit gibier de plaine chassée en France (Aubry et al., 2016; Bro, Reitz, & Landry, 2005). Son importance est à la fois culturelle et socio-économique (Aebischer et al., 2003; Bro, 2016).

Aujourd'hui, elle bénéficie d'un « statut de conservation défavorable », considérée comme vulnérable à l'échelle de l'Europe (Hagemeijer & Blair, 1997; Tucker & Heath, 1994), en raison d'un déclin marqué des abondances sur l'ensemble de la zone dont elle est native et d'une contraction de son aire de distribution depuis les années 1950-1970 (Encart 3 ; Aebischer & Potts, 1994). La Perdrix grise est donc listée dans la liste rouge des espèces préoccupantes en termes de conservation au Royaume-Uni (Eaton et al., 2015, 2009), et est intégrée parmi les 19 espèces constituant le « Farmland Bird Indicator », parmi lesquelles elle

représente l'espèce la plus étudiée (Aebischer et al., 2003). La population française de Perdrix grise, classée en « Préoccupation Mineure » (« Least Concern » ; UICN France, MNHN, LPO, SEOF, & ONCFS, 2016) en raison de son abondance la plus importante d'Europe de l'Ouest (elle représente à elle seule 47% des effectifs européens ; Bro, 2016; voir aussi Aebischer & Kavanagh, 1997; BirdLife International, 2004), a été identifiée comme essentielle et centrale dans la conservation et le futur de l'espèce en Europe (Bro & Crosnier, 2012; Bro et al., 2005).

Encart 3 La Perdrix grise : l'historique du déclin en quelques chiffres

En Europe, les populations de Perdrix grise sont en déclin depuis la fin des années 1950 (ou années 1960-70 en Europe continentale) (Aebischer & Kavanagh, 1997; Aebischer & Potts, 1994; Bro, 2016; Kuijper, Oosterveld, & Wymenga, 2009). À la fin des années 1990, les niveaux de population ne représentent plus que 10-20% des effectifs d'avant-guerre dans de nombreux pays : Royaume-Uni, Pays-Bas, Allemagne, Italie, Autriche, Hongrie (Aebischer & Kavanagh, 1997; Aebischer & Potts, 1994). La Perdrix grise tend vers l'extinction en Irlande et en Suisse, et a disparu en Norvège, au Portugal, au nord-ouest de l'Espagne, au sud de l'Italie et au sud de la Grèce (Aebischer & Kavanagh, 1997; Aebischer & Potts, 1994; Sotherton, Aebischer, & Ewald, 2010). Au Royaume-Uni où les tendances populationnelles sont particulièrement bien étudiées (prélèvements de chasse recensés depuis 1793 ; Potts & Aebischer, 1995), un déclin marqué de 92% en abondance est observé entre 1970 et 2015 (Hayhow et al., 2017), ainsi qu'une contraction estimée de 19% de son aire de distribution entre 1970 et 1990 (Sotherton et al., 2014). La population du Royaume-Uni était alors estimée à 70- 75 000 couples en 2000 (Baillie et al., 2010), 43 000 couples en 2009 (Bro, 2016).

Les populations française et polonaise auraient décliné dans une moindre mesure (Aebischer & Kavanagh, 1997; Aebischer & Potts, 1994; Bro, 2016). En France, un déclin de 20% en abondance est observé entre 1970 et 1990 (Bro, 2016). À partir de la fin des années 1980, les tendances annoncées divergent : déclin de 23% en abondance entre 1989 et 2015 (Vigie-Nature, 2018), déclin de 11% en abondance et contraction de 20% de son aire de distribution entre 1985 et 2013 (Comolet-Tirman et al., 2015), ou relative stabilité (Bro, 2016; Bro & Crosnier, 2012). Le nombre de reproducteurs en France était estimé à 900 000 couples en 1986 (Aebischer & Potts, 1994), 750 000 au printemps 1998 (Reitz, 2003) et 800 000 en 2008 (Bro & Crosnier, 2012). Cependant, les populations de Perdrix grise sont aujourd'hui maintenues par des lâchers d'oiseaux d'élevage sur une grande partie du territoire français (Fig. 4 ; Bro & Crosnier, 2012).

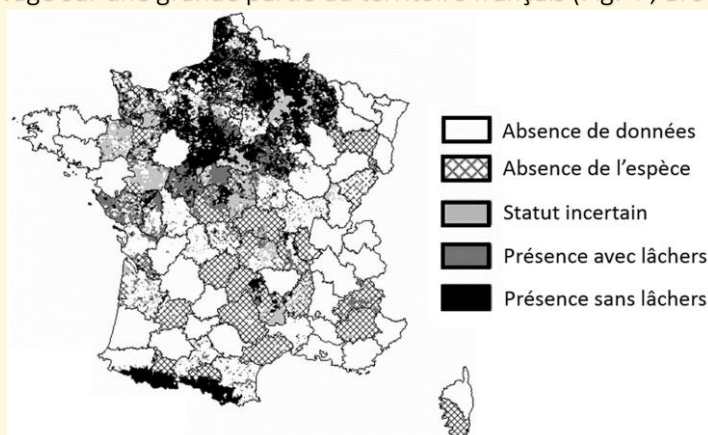


Figure 4 Distribution de la Perdrix grise en France au printemps 2008 selon le statut des populations (naturelles *versus* maintenues par lâchers). 'Statut incertain' correspond aux populations pour lesquelles l'une des informations (abondance ou pratique de lâcher) est manquante. Source : Bro & Crosnier (2012).

2. Une espèce en déclin : de la cause initiale aux causes émergentes

En raison de son statut d'espèce emblématique, les origines du déclin de la Perdrix grise ont été très étudiées. La plupart des causes identifiées sont liées de manière directe ou indirecte à l'intensification de l'agriculture (Aebischer & Potts, 1994), mais ces causes ont varié au cours du temps. Aebischer & Ewald (2012) identifient trois causes majeures, liées à l'intensification de l'agriculture : la destruction de l'habitat de nidification, la chute de disponibilité en insectes nécessaires à l'alimentation des juvéniles, et dans une phase plus récente, la pression de prédation accrue dans les habitats restants.

Avant les années 1950, les fluctuations démographiques des populations de Perdrix grise dépendaient essentiellement de l'influence des conditions climatiques sur la survie juvénile et adulte (Fig. 5 ; Kuijper et al., 2009; voir aussi Bro, 2016). La première phase de déclin des populations de Perdrix grise survient entre les années 1950 et 1990 (1950 à 1970 au Royaume-Uni, 1960-70 à 1980-90 dans le reste de l'Europe dont la France ; Aebischer & Potts, 1994; Bro, 2016; Kuijper et al., 2009), par une diminution considérable du succès reproducteur (Gée, Sarasa, & Pays, 2018; Kuijper et al., 2009). La réduction de la disponibilité en insectes engendrée par l'intensification de l'agriculture (via la modification des paysages et l'utilisation massive des pesticides), est identifiée comme cause principale de ce déclin, affectant la survie des juvéniles après éclosion (Kuijper et al., 2009; Potts, 1980; Potts & Aebischer, 1991). Des événements climatiques exceptionnels (hivers rigoureux, printemps froids et/ou humides) auraient également affecté la survie hivernale des adultes et le succès reproducteur (Bro, 2016). Bien que la contribution de la chasse soit relativement peu documentée et considérée comme mineure dans la première phase du déclin de cette espèce gibier, les prélèvements cynégétiques auraient également contribué au déclin des populations, au moins dans certaines régions à forte pression de chasse (exemple de la sous espèce *Perdix perdix italica* H. 1917 en Italie ; Lovari, 1975; Renzoni, 1974; voir aussi R. A. Fuller, Carroll, & McGowan, 2000).

À partir des années 1980-90 s'initie une seconde phase du déclin dans des habitats dégradés et fragmentés par l'intensification agricole (Fig. 5 ; Kuijper et al., 2009; voir aussi Bro, 2016). Ces nouvelles causes affectent à la fois les paramètres de survie et de reproduction (Fig. 5 ; De Leo, Focardi, Gatto, & Cattadori, 2004; Kuijper et al., 2009; Panek, 2005). La survie des adultes (femelles en couvaison, en période de chasse, et hivernale) devient le principal déterminant de la croissance démographique, alors que les paramètres de reproduction

(succès d'éclosion, taille des couvées, survie juvénile) deviennent secondaires (Bro, Sarrazin, Clobert, & Reitz, 2000). Cette mortalité accrue est principalement attribuée à la prédation (Bro, Reitz, Clobert, Migot, & Massot, 2001; Kuijper et al., 2009; Panek, 2005; Potts, 1980). La mortalité par prélèvement devient également un important déterminant de la croissance démographique dans les populations affaiblies, avec un effet potentiellement supérieur à celui de la prédation en période de chasse (Besnard, Novoa, & Gimenez, 2010; Bro, Sarrazin, et al., 2000; M. Watson, Aebischer, Potts, & Ewald, 2007). La stochasticité climatique est également citée comme l'une des menaces pesant sur les populations affaiblies. Des événements pluvieux associés à des températures froides entre mi-juin et mi-juillet affecteraient le succès reproducteur, favorisant des abandons de couvées, mais aussi une mortalité accrue des poussins dans les semaines qui suivent l'éclosion (Bro, Brillard, & Millot, 2014; Panek, 1992; Pépin, Birkan, & Angibault, 2008; Potts & Aebischer, 1995).

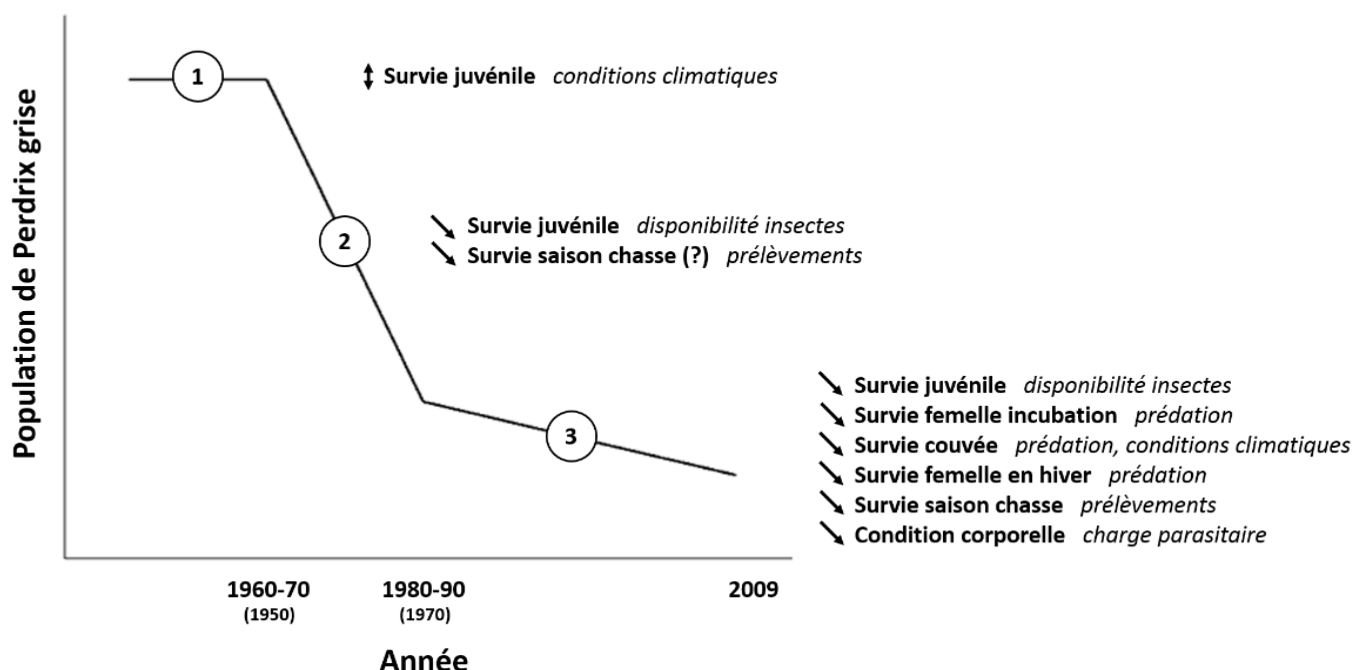


Figure 5 Schéma représentant les trois phases du déclin de la Perdrix grise en Europe, les paramètres démographiques limitants (en gras), leur tendance ($\uparrow$: fluctuation, $\searrow$: diminution), et les facteurs principaux qui les affectent (en italique). Les dates correspondent aux périodes de déclin observées en Europe continentale, les dates entre parenthèses correspondent aux périodes de déclin observées au Royaume-Uni. Réalisé à partir de Kuijper et al. (2009), modifié selon Aebischer & Potts (1994), Bro (2016), Bro et al. (2014), Gée et al. (2018).

3. Situation actuelle : des populations affaiblies sur des territoires dégradés

De lâchers de repeuplement vers des lâchers cynégétiques

Face au déclin de l'espèce, les opérations de renforcement de populations (ou repeuplements) voire de réintroduction se sont multipliées (Bro & Mayot, 2006; Browne, Buner, & Aebischer, 2009; Buner, 2009; Buner, Brockless, & Aebischer, 2013; Lanz, Michler, & Duplain, 2012). Ces opérations consistaient en des lâchers d'oiseaux associés à une suspension de la chasse (Bro, 2016), sur des territoires dont la capacité d'accueil n'était pas atteinte (Bro & Mayot, 2006), parfois couplées à un aménagement de l'habitat (Buner et al., 2013; Lanz et al., 2012). En France, bien que majoritairement bénéfiques à court terme (augmentation des effectifs dans 90% des cas ; Bro, 2016), ces opérations se sont révélées moins efficaces sur le long terme (seulement 27% des améliorations des densités encore visibles après 10 ans ; Bro, 2016). Devant ces échecs et la perte de motivation des chasseurs qu'ils engendrent (Bro, 2016), une dérive des pratiques vers des lâchers cynégétiques annuels d'oiseaux d'élevage (conspécifiques ou espèces non-natives ; Carpio et al., 2017; Champagnon, Elmberg, Guillemain, Gauthier-Clerc, & Lebreton, 2012; Sokos, Birtsas, & Tsachalidis, 2008) sans suspension de la chasse est observée, notamment dans les zones de faible densité (« lâchers d'été » avant la saison de chasse, ou « lâchers de tir » au cours de la saison de chasse ; Bro & Mayot, 2006; Bro, Mayot, & Mettaye, 2006; voir aussi Sokos et al., 2008 pour une discussion sur la généralisation de cette pratique chez les Galliformes). À l'origine, cette pratique visait à motiver les chasseurs à gérer leurs territoires grâce au maintien de l'activité cynégétique (Bro, Mayot, et al., 2006). En réalité cette pratique pourrait se révéler contre-productive, habituant les chasseurs à des tableaux de chasse relativement élevés quel que soit le succès reproducteur de l'année, sans aucune nécessité de gérer leurs territoires (Bro, Mayot, et al., 2006; ONCFS, 2014). Mais à ce jour, qu'en est-il de la qualité de l'habitat ? Pourrait-elle être devenue limitante pour soutenir ces populations d'oiseaux ?

Des lâchers d'espèces non-natives : une compétition suggérée, jamais démontrée

Une première forme de lâcher cynégétique repose sur des introductions d'espèces non-natives et chassables (par exemple la Perdrix rouge *Alectoris rufa* L. 1758, la Perdrix choukar *Alectoris chukar* G. 1830, le Faisan de Colchide *Phasianus colchicus* L. 1758 ; Aebischer & Ewald, 2004, 2010; Bro & Mayot, 2006; Renzoni, 1974; P. A. Robertson, 1996). Ces introductions d'espèces à but cynégétique ont été très largement réalisées en Europe (Carpio

et al., 2017; Jeschke & Strayer, 2006; McCabe & Hawkins, 1946; Musil & Connelly, 2009; P. A. Robertson, 1996), et plus particulièrement en Europe de l'Ouest (plus de 20 espèces introduites en France, au Royaume-Uni, en Allemagne et en Italie ; Carpio et al., 2017), impliquant plusieurs espèces phylogénétiquement proches (majoritairement des *Phasianidae* appartenant à l'ordre des Galliformes ; Carpio et al., 2017; voir aussi Blackburn & Duncan, 2001). Cependant, les impacts de cette pratique sur la biodiversité locale restent mal connus, et cette question a été identifiée parmi les 100 questions écologiques d'importance politique majeure au Royaume-Uni (Sutherland et al., 2006; voir aussi Bicknell et al., 2010).

Actuellement réalisée dans le but de relâcher la pression de chasse pesant sur les populations d'espèces natives d'intérêt cynégétique en déclin (Aebischer & Ewald, 2004; Bro, 2016; Carpio et al., 2017), cette pratique est remise en cause car elle pourrait en réalité se révéler contreproductive pour plusieurs raisons : tirs par inadvertance sur l'espèce à préserver (voir Aebischer & Ewald, 2010 pour la Perdrix grise), propagation et transmission de pathogènes (Díaz-Sánchez, Moriones, Casas, & Höfle, 2012; Tompkins, Greenman, Robertson, & Hudson, 2000; Villanúa et al., 2008), susceptibles d'affecter la condition corporelle des individus dans les populations cibles (voir Tompkins, Draycott, & Hudson, 2000 pour un exemple de transmission de parasites, ou compétition indirecte médiée par le parasitisme du Faisan de Colchide à la Perdrix grise), hybridations (Barbanera et al., 2015; Barilani et al., 2007). Cependant, alors que ces introductions impliquent un apport d'individus d'espèces phylogénétiquement et écologiquement proches de la Perdrix grise (*Phasianidae* ; Blackburn & Duncan, 2001; Carpio et al., 2017), sur les mêmes territoires dont la quantité et la qualité des habitats (et donc la capacité d'accueil) auraient diminué (Aebischer & Ewald, 2012), l'hypothèse de compétition interspécifique reste étonnamment peu documentée. Pourtant, selon les prédictions de Hardin (1960), la remise en contact par introduction de deux espèces anciennement séparées (c'est-à-dire biogéographiquement, par leur passé évolutif) devrait mener soit à l'extinction de l'une des espèces par la seconde, soit à la coexistence sous réserve de la mise en place de différenciations écologiques lors de la mise en contact de ces deux espèces.

De telles relations de compétition interspécifique ont été suggérées à plusieurs reprises dans les milieux agricoles (notamment Perdrix grise - Perdrix rouge : Meriggi, Montagna, & Zacchetti, 1991; P. A. Robertson, 1996; et Perdrix grise - Faisan de Colchide : Renzoni, 1974; P. A. Robertson, 1996; voir aussi Bro, 2016), mais restent discutées et non démontrées (Bro,

2016; Meriggi et al., 1991; Potts, 1980; Renzoni, 1974; P. A. Robertson, 1996). Bro (2016) relève notamment qu'aucune étude approfondie n'a été menée pour examiner l'existence d'une relation de compétition interspécifique entre Perdrix grise et Perdrix rouge.

Les Perdrix grise et rouge sont deux espèces phylogénétiquement (Wang, Kimball, Braun, Liang, & Zhang, 2013) et écologiquement (Bro & Ponce-Boutin, 2004; Green, 1984b; Green et al., 1987; Rands, 1988) proches. Leurs aires de distribution originellement distinctes mais contiguës (Bull, 1991; Cramp & Simmons, 1980; G. E. Watson, 1962), suggéraient une parapatrie compétitive (Bull, 1991; G. E. Watson, 1962). La zone de contact entre leurs aires de distribution était restreinte au centre et au sud de la France, ainsi qu'au nord-ouest de l'Italie (Cramp & Simmons, 1980). De par les lâchers massifs de Perdrix rouge au Royaume-Uni et en France, cette zone de contact s'est considérablement étendue (Cramp & Simmons, 1980). Les apports de Perdrix rouge dans le but de préserver les populations de Perdrix grise sont réalisés sur l'ensemble du territoire français (Bro & Mayot, 2006; Ponce-Boutin, Crosnier, & Reitz, 2012; Reitz, 2003). Entre 1998 et 2006, une expansion de la distribution de la Perdrix rouge est observé vers le nord de la France dans des territoires où elle n'était pas présente jusqu'alors (Ponce-Boutin et al., 2012; Reitz, 2003). Alors qu'un déclin de 23% de la Perdrix grise est observé entre 1989 et 2015, le déclin de Perdrix rouge se limite à 3% sur cette même période, compensé par l'augmentation des densités au nord (Ponce-Boutin et al., 2012). Dans le contexte actuel de populations déjà très affaiblies dans des paysages agricoles intensifiés, la présence et les introductions massives et répétées d'espèces gibiers non-natives, phylogénétiquement et écologiquement proches de la Perdrix grise, pourraient-elles constituer un facteur aggravant et limiter son accès à l'habitat, à la ressource, et par conséquent le recouvrement de ses populations ?

Des lâchers d'individus issus d'élevage

Face à la diminution des effectifs d'espèces d'intérêt cynégétique, le renforcement des populations par des individus conspécifiques issus d'élevage constitue une seconde forme de lâcher communément réalisée dans les régions à faible densité de population (Bro & Crosnier, 2012; Bro, Mayot, et al., 2006; Champagnon, Elmberg, et al., 2012; Champagnon, Guillemain, Gauthier-Clerc, Lebreton, & Elmberg, 2013; Ponce-Boutin, Brun, Mathon, & Ricci, 2006; Sokos et al., 2008). Le nombre de Perdrix grises d'élevage lâchées annuellement est estimé à 2 millions pour chacune des années 1995, 2008 et 2015 en France, 30 000 à 35 000 par an en

Pologne sur la période 2005-2010, 20 000 à 70 000 au Danemark (Bro, 2016). Ce type de gestion par lâchers cynégétiques d'oiseaux d'élevage sans suspension de la chasse est dite « gestion mixte » en raison des « populations mixtes » qui en résultent (populations sauvages supplémentées annuellement par des oiseaux issus d'élevage) (Bro & Mayot, 2006; Bro, Mayot, et al., 2006; Mayot, 2006). Cependant, cette pratique semble inefficace pour recouvrer ou maintenir des niveaux de populations viables (Bro, Mayot, et al., 2006), et étant donné que les prélèvements s'exercent aussi bien des individus issus d'élevage que des individus sauvages (Bro, Mayot, et al., 2006; Mauvy, Lartiges, Valery, & Peroux, 1992; Ponce-Boutin et al., 2006), elle pourrait, à terme, mener à une disparition des populations sauvages et à un remplacement par des populations constituées essentiellement d'oiseaux d'élevage (Bro, Mayot, et al., 2006; ONCFS, 2014; Ponce-Boutin et al., 2006).

Or, la reproduction en captivité à long terme engendre une perte de variabilité génétique (Ewen et al., 2012; Keller, Biebach, Ewing, & Hoeck, 2012). Cette perte de variabilité génétique (et immunogénétique ; Ewen et al., 2012; Keller et al., 2012), entraînerait une diminution de la diversité des types comportementaux exprimés dans les populations renforcées (la répétabilité et l'héritabilité de la personnalité, du comportement de prise de risque et du comportement exploratoire suggèrent une base génétique ; Dingemanse, Both, Drent, van Oers, & van Noordwijk, 2002; van Oers, de Jong, et al., 2004; van Oers, Drent, et al., 2004), et de leur vulnérabilité face aux pathogènes, ce qui pourrait altérer leurs capacités d'ajustement et d'adaptation rapide aux changements environnementaux (introduction de prédateur, maladies, compétition, changements abiotiques ; Ewen et al., 2012; Keller et al., 2012; Watters & Meehan, 2007).

Bien que plusieurs limites à cette pratique aient été identifiées (introgression génétique dans les populations locales menaçant certaines sous-espèces telles que *Perdix perdix hispaniensis* R. 1892; Bech, Novoa, Bro, & Boissier, 2012; *Perdix perdix italica* H. 1917 Lovari, 1975; déficiences physiologiques des individus d'élevage pour répondre au stress alimentaire ; Homberger, Jenni-Eiermann, Roulin, & Jenni, 2013), les déficiences comportementales dans le comportement anti-prédateur (réduction de 50% du temps alloué à la vigilance comparé aux individus sauvages ; Rantanen, Buner, Riordan, Sotherton, & Macdonald, 2010b) ont été identifiées comme cruciales, et responsables de la forte mortalité post-lâcher de ces oiseaux par prédation (60 à 80% ; Bro, 2016; 82% dans Parish & Sotherton, 2007; 77% dans Rymesova, Tomasek, & Salek, 2013; voir aussi Sokos et al., 2008). En raison de ces comportements anti-

prédateurs inadéquats, les individus utiliseraient des habitats associés à un fort risque de prédation et souffriraient une mortalité accrue (Rantanen, Buner, Riordan, Sotherton, & Macdonald, 2010a). Des différences morphologiques (longueur de l'aile plus courte, condition corporelle plus faible ; Rymesova et al., 2013), pourraient également altérer leurs compétences de vol (angle de décollage plus faible lors de la fuite, prennent de l'altitude moins vite et volent moins loin que des oiseaux sauvages ; Rymesova, Smilauer, & Salek, 2012), et les rendre plus vulnérables face à la prédation (Putala, Oksa, Rintamäki, & Hissa, 1997; Rymesova et al., 2012).

L'augmentation de la prévalence de ces oiseaux d'élevage dans les populations (apports annuels associés aux prélèvements s'exerçant sur les individus sauvages ; Bro, 2016; Bro, Mayot, et al., 2006; Mauvy et al., 1992; ONCFS, 2014), pourraient donc également modifier le comportement de prise de risque et de sélection de l'habitat au niveau populationnel, et affecter la capacité d'ajustement des populations mixtes aux perturbations et aux changements environnementaux. Alors qu'une demande croissante de lâchers sans suspension de chasse a été observée (Bro, Mayot, et al., 2006; voir aussi Sokos et al., 2008), l'impact de ce mode de gestion sur les populations reste méconnu (Bro, Mayot, et al., 2006). Il existe donc aujourd'hui une nécessité d'identifier et comprendre les limites de cette gestion, ainsi que d'évaluer la capacité d'ajustement comportemental de ces populations aux pressions de leur environnement (prédation, forte dynamique des paysages, activités humaines dont l'activité cynégétique), comme potentielle limite au recouvrement des populations.

IV. Objectifs et organisation de la thèse

1. Problématique

Le processus comportemental de sélection de l'habitat est influencé par la variation des stimuli environnementaux tels que disponibilité en habitats (couvert d'alimentation, refuges, sites de nidification) et la présence de menaces (compétiteurs, prédateurs). Dans les environnements soumis aux changements anthropiques rapides tels que les milieux agricoles, l'ensemble de ces stimuli ont été altérés (perte et dégradation des habitats, redistribution infra-annuelle des couverts végétaux, modification en conséquence des interactions interspécifiques), affectant les dynamiques des populations d'oiseaux. Bien que la

compréhension des réponses comportementales des populations ait été identifiée comme essentielle pour la conservation et la gestion des populations (permettant notamment d'identifier et d'appréhender les facteurs limitant les populations), les mécanismes d'ajustement comportemental à ces changements environnementaux restent méconnus et peu documentés.

Cette étude s'intéresse à la Perdrix grise, l'une des espèces indicatrices des milieux agricoles les mieux étudiées (Aebischer et al., 2003) dont la situation est préoccupante en Europe. L'enjeu principal est d'identifier les facteurs limitant le recouvrement des populations (changements paysagers, pratiques cynégétiques), et de caractériser la réponse des populations à ces facteurs, dans le but de proposer des pistes d'amélioration en termes de gestion des populations. Nos objectifs se sont focalisés plus précisément sur trois points inexplorés à ce jour : l'influence de la dynamique temporelle de l'habitat dans les paysages agricoles intensifs, de la compétition interspécifique, et de la structuration spatiotemporelle des perturbations naturelles et anthropiques (via l'apport de la technologie GPS chez cette espèce), sur le processus comportemental de sélection de l'habitat.

2. Cadre de l'étude

Cette étude s'insère dans un contexte novateur car peu étudié jusqu'alors bien qu'il tende à se généraliser (Bro & Crosnier, 2012; Bro & Mayot, 2006; Bro, Mayot, et al., 2006), malgré une mise en doute de son efficacité pour le maintien des populations (Bro, Mayot, et al., 2006) : l'étude d'une population de faible densité, essentiellement gérée et maintenue par lâchers cynégétiques annuels d'oiseaux d'élevage.

3. Axes de recherche

Cette thèse se structure en quatre axes:

Axe 1 Effet des changements paysagers sur le processus de sélection de l'habitat : la qualité de l'habitat peut-elle être limitante ?

Dans un paysage agricole en intensification, une perte de quantité et de qualité des habitats favorables est attendue au cours du temps. Des changements dans les patrons de sélection de l'habitat devraient donc être observés en conséquence (Arthur, Manly, McDonald, & Garner, 1996; López-Jamar et al., 2011; Panek & Kamieniarz, 2000). Cependant,

les lâchers annuels d'oiseaux d'élevage, souvent caractérisés par des déficiences comportementales multiples (Rantanen et al., 2010b, 2010a; Sokos et al., 2008), pourraient également être déterminants dans le processus de sélection de l'habitat et contraindre de tels ajustements (incapacité à s'ajuster ?). Devant le déclin continu des populations de Perdrix grise, on peut s'attendre à ce que les ajustements ne soient pas adéquats ou suffisants pour répondre favorablement aux changements environnementaux (Gilroy et al., 2011; Sih et al., 2011).

Le Chapitre I consiste en une analyse temporelle (1997 – 2017) des patrons de sélection de l'habitat au niveau populationnel, en relation avec la dynamique des paysages agricoles. Les principaux déterminants paysagers influençant la présence de Perdrix grise ainsi que leurs effets respectifs seront quantifiés. Les changements des patrons de sélection de l'habitat au cours du temps seront analysés. La dynamique temporelle de la qualité de l'habitat sera évaluée et confrontée aux ajustements observés, et discutée comme l'un des facteurs explicatifs.

Axe 2 La compétition interspécifique pourrait-elle affecter l'accès à la ressource ? - Le cas de la relation Perdrix grise – Perdrix rouge

Dans les agrosystèmes intensifs, la qualité de l'habitat a diminué et des pressions de compétition exacerbées sont attendues pour des ressources (habitat, alimentation) de plus en plus limitantes (Newton, 2004; Robillard et al., 2013; Sih et al., 2011). L'apport artificiel et annuel d'oiseaux d'espèces phylogénétiquement et écologiquement proches de la Perdrix grise, originellement parapatriques, telles que la Perdrix rouge, pourrait constituer un facteur aggravant additionnel (Bro, 2016; Carpio et al., 2017; Hardin, 1960; Renzoni, 1974). Nos prédictions sont que l'augmentation artificielle de la zone de contact entre ces deux espèces, conduit à une situation de compétition interspécifique par interférence, dans laquelle la Perdrix grise (plus petite) serait dominée par la Perdrix rouge (plus massive) (P. R. Martin et al., 2017; Persson, 1985). Des conséquences asymétriques sont attendues sur l'accès à l'habitat, qui devrait être altéré pour l'espèce dominée (Perdrix grise) (P. R. Martin et al., 2017; P. R. Martin & Martin, 2001b).

L'objectif du Chapitre II est d'analyser l'existence et les conséquences d'une compétition interspécifique entre les Perdrix grise et rouge. Une analyse comparative des comportements territoriaux en réponse aux chants hétérospécifique *versus* conspécifique, et des niches des

deux espèces en situations d'absence ou de co-occurrence du potentiel compétiteur seront réalisées.

Axe 3 Variation spatiotemporelle des perturbations naturelles (prédation) et anthropiques (chasse) : quelle influence sur la sélection de l'habitat, l'utilisation de l'espace, et la survie ?

Le processus de sélection de l'habitat est influencé par le risque de prédation. Dans les paysages anthropisés tels que les milieux agricoles, les activités humaines (activités agricoles, activité cynégétique) s'ajoutent aux perturbations naturelles et modifient la structuration spatiotemporelle du risque. Au niveau populationnel, on devrait donc s'attendre à observer une variation des patrons de sélection de l'habitat en réponse à la structuration des perturbations (Lone et al., 2015; Norum et al., 2015; Pan et al., 2011). Cependant, lors des opérations de lâcher, les oiseaux sont naïfs vis-à-vis de ce nouvel environnement hétérogène, fortement dynamique, soumis à de multiples pressions (prédation, activités humaines), et accusent une forte mortalité (Rantanen et al., 2010b; Sokos et al., 2008). La survie des individus pourrait donc être conditionnée par leur capacité d'ajustement comportemental en réponse à la structuration spatiotemporelle des pressions (Lone et al., 2015). Nous nous attendons donc à observer des différences de performance individuelle (survie) en fonction des comportements de sélection de l'habitat et de déplacement des individus.

À partir d'un suivi GPS d'individus d'élevage en phase post-lâcher, l'objectif de cet axe est d'analyser les mécanismes fins d'ajustement de la sélection de l'habitat et des déplacements, en relation avec la structuration spatiotemporelle des pressions environnementales (risque de prédation par les carnivores, activités humaines) (Chapitre III). Les variations des rythmes d'activité de déplacement, de sélection de l'habitat et d'utilisation de l'espace, ont été analysées au cours du cycle circadien. Des ajustements comportementaux aux variations du risque (prédation nocturne par les carnivores, activités humaines diurnes) devraient être observés, a minima chez les individus survivants. Une analyse de la sélection de l'habitat (distance aux habitats associés à un fort risque de prédation) en fonction de la survie des individus (survivants, prédatés, chassés) sera également réalisée.

Axe 4 Influence des traits individuels sur la capacité d'ajustement de la sélection de l'habitat à la structuration des perturbations environnementales

Dans les paysages hétérogènes, la structuration spatiotemporelle de la ressource et des perturbations (prédation, activités humaines) incite les individus à se déplacer et à ajuster leur sélection de l'habitat (Lone et al., 2014, 2015; Pan et al., 2011; Tolon et al., 2009). Sachant que les traits individuels (personnalité, caractéristiques morphologiques, état sanitaire) influencent la perception et/ou la réponse au risque (López & Martín, 2015; Martín, De Neve, Polo, Fargallo, & Soler, 2006; Nathan et al., 2008; Sih & Del Giudice, 2012), on devrait s'attendre à observer des différences interindividuelles dans les capacités d'ajustement de la sélection de l'habitat à la structuration spatiotemporelle des risques (naturels, anthropiques) (Bonnot et al., 2014; Holtmann et al., 2017). Ces différences devraient être influencées par les traits individuels.

Dans un chapitre prospectif (Chapitre IV), nous avons exploré l'influence de plusieurs déterminants individuels (personnalité, caractéristiques morphologiques, état sanitaire) sur l'ajustement de la sélection de l'habitat à la variation des perturbations environnementales.

Méthodes générales

I. Sites d'étude

L'ensemble des chapitres de cette thèse repose, pour tout (Chapitres I, III & IV) ou partie (Chapitre II) des données, sur la Zone Atelier « Plaine & Val de Sèvre » (ZAPVS, Fig. 6b ; Bretagnolle et al., 2018b). Sur cette zone de 435 km², caractérisée par une agriculture céréalière intensive, l'occupation du sol est recensée depuis 1994. Composée d'environ 19000 parcelles en 1996 (550 exploitations), elle en comporte environ 13000 aujourd'hui. L'occupation du sol est largement dominée par les céréales d'hiver, qui représentent 41,5% de la zone (surface moyenne estimée sur les années 2009 à 2016 ; Bretagnolle et al., 2018b). Les autres cultures et types d'occupation du sol majoritaires sont le tournesol (10,4%), le maïs (9,6%), le colza (8,3%), ainsi que les milieux prairiaux (13,5%). Les boisements et les zones bâties représentent respectivement 2,9% et 9,8%. Une intensification des pratiques agricoles a été enregistrée sur la ZAPVS, notamment caractérisée par une augmentation de 20% de la surface en céréales depuis 1994 (Bretagnolle et al., 2018b).

Plus de la moitié de cette zone est désignée comme site NATURA 2000 depuis 2003, dans le but de protéger 17 espèces de la Directive Oiseaux, telles que l'Outarde canepetière *Tetrax tetrax* L. 1758 (Bretagnolle et al., 2018b). Le statut « Zone Atelier » est obtenu en 2008, et l'intègre parmi un réseau de zones d'études, gérées par le Centre National de la Recherche Scientifique (CNRS), et impliquées dans une démarche de recherches pluridisciplinaires sur le long terme (Bretagnolle et al., 2018b; Lévêque, Pavé, Abbadie, Weill, & Vivien, 2000).

Une seconde zone d'étude de 18 km², située dans le sud du département du Maine-et-Loire (Fig. 6a), a également été prospectée dans le but d'augmenter les contacts de Perdrix grise et rouge dans le cadre du Chapitre II. Cette seconde zone d'étude a été sélectionnée selon deux critères : (1) proximité de la ZAPVS pour garantir une homogénéité dans la phénologie des cultures et du cycle de reproduction des oiseaux, (2) être caractérisée par les mêmes faciès paysagers (agriculture céréalière intensive avec les mêmes types d'habitats, dans des proportions similaires). En 2017, sur cette zone, l'occupation du sol était majoritairement représentée par des céréales d'hiver (42,4%). Les autres cultures et principaux types d'occupation du sol sont les maïs et tournesol (29,7%), le colza (7,9%), les milieux prairiaux (8,5%), les boisements (4,2%) et le bâti (3,6%, en excluant la ville de Doué-la-Fontaine au sud de la zone d'étude).

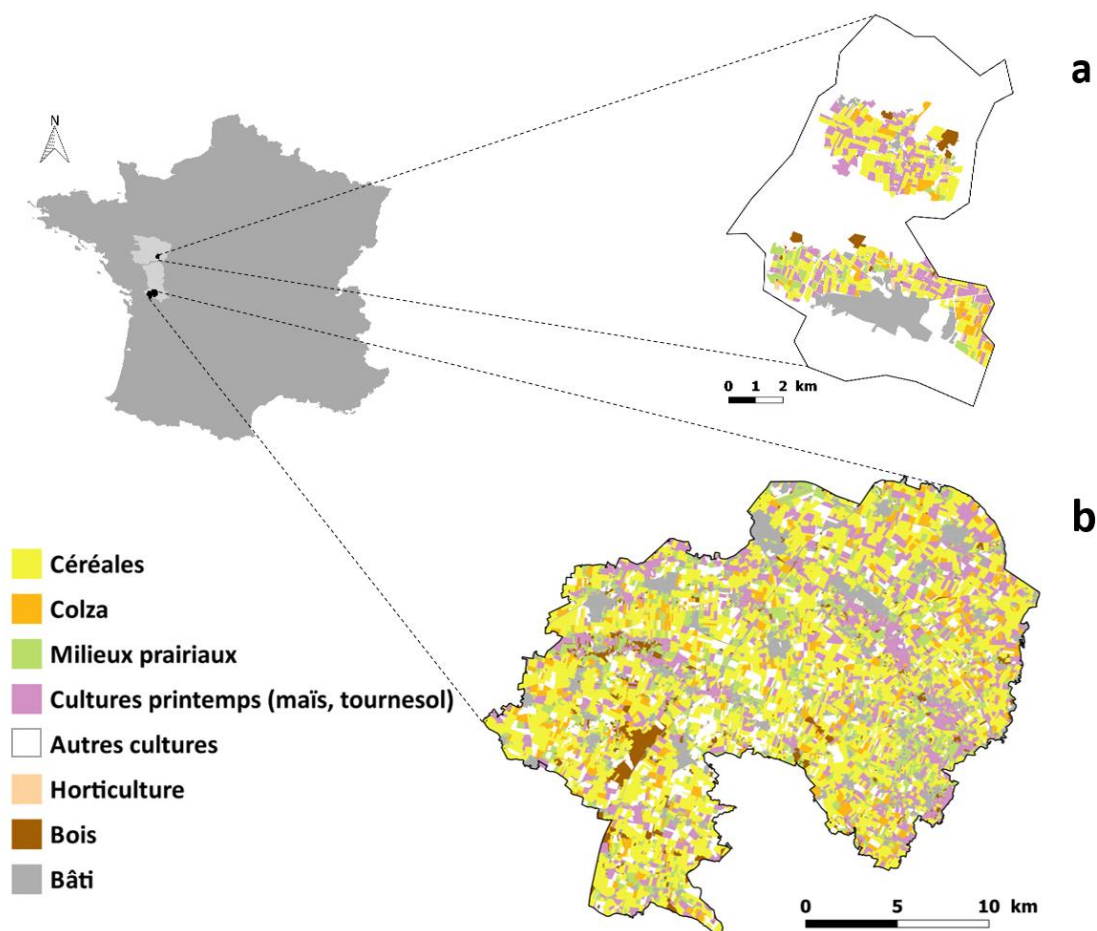


Figure 6 Localisation des zones d'études prospectées dans le cadre de cette étude. (a) correspond à l'un des sites prospectés dans le cadre du Chapitre II, situé dans le département du Maine-et-Loire (Pays-de-la-Loire, France) ; (b) correspond à la zone d'étude principale, la Zone Atelier « Plaine & Val de Sèvre » (Long-Term Socio-Ecological Research platform, LTSER) située dans le département des Deux-Sèvres (Nouvelle-Aquitaine, France), sur laquelle l'ensemble des chapitres de cette étude se sont basés. Les codes couleurs font références à l'occupation du sol recensée sur ces deux sites en 2017.

II. Protocoles expérimentaux

1. Observations ornithologiques

La collecte des observations d'oiseaux est réalisée sur la ZAPVS depuis 1995 et prend deux formes : des points d'écoute standardisés et réalisés annuellement, et des observations dites *ad libitum* ou opportunistes, collectées lorsqu'un ornithologue observe un oiseau en dehors des protocoles standardisés de points d'écoute.

Le protocole standardisé de points d'écoute consiste en des points fixes dans le temps, échantillonnés chaque année entre 1995 et aujourd'hui (Brodier, Augiron, Cornulier, & Bretagnolle, 2014). Le nombre de points d'écoute échantillonnés a toutefois augmenté au cours du temps, de 160 (1995-2008) à environ 450 depuis 2009, répartis sur l'ensemble de la

ZAPVS (Bretagnolle et al., 2018a). La durée des points d'écoute est de 5 ou 10 minutes (Brodier et al., 2014), réalisés entre 7h00 et 11h00 du matin, sans utilisation de repasse audio. Bien que ce protocole n'ait pas été développé dans le cadre de cette thèse, les données collectées ont été utilisées.

En parallèle de ce protocole, des données non-protocoles sont consignées chaque année. Entre mars et juillet, lorsque les ornithologues du Centre d'Etudes Biologique de Chizé observent des oiseaux en dehors du protocole de points d'écoute, ces données sont reportées et consignées dans une base de données. Une partie de ces observations est réalisée lors du recensement de l'occupation du sol, qui consiste en deux passages par saison sur l'ensemble des parcelles de la zone atelier afin de reporter les cultures présentes.

Bien que ces protocoles de collecte de données n'aient pas été développés dans le cadre de cette thèse, les données ont été utilisées dans le cadre des Chapitres I & II pour la modélisation de distribution d'espèce (Chapitre I) et la modélisation de niches (Chapitre II).

2. Points d'écoute Perdrix

Dans le but d'étudier l'existence et les effets d'une compétition Perdrix grise – Perdrix rouge (Chapitre II), un protocole de points d'écoute Perdrix a été développé et appliqué en 2016 (140 points sur la ZAPVS) et 2017 (275 points sur la ZAPVS et 75 dans le Maine-et-Loire, Fig. 6). L'objectif est d'étudier les comportements territoriaux des deux espèces de Perdrix, lors de la diffusion de chants conspécifique (chant de leur propre espèce) et hétérospécifique (chant d'une autre espèce, en l'occurrence de la seconde espèce de Perdrix).

Le protocole consiste en des points d'écoute standardisés, disposés à environ 500 m les uns des autres (situés en bord de route ou de chemin pour faciliter l'accès et éviter le dérangement des oiseaux avant échantillonnage), sur lesquels sont diffusés dans un ordre aléatoire les chants de Perdrix grise, Perdrix rouge, et un chant témoin (Caille des blés *Coturnix coturnix* L. 1758). Chaque point d'écoute a été échantillonné 4 fois par saison, deux fois le matin (entre 7h00 et 11h00) et deux fois le soir (entre 17h00 et 21h00) étant donné que l'activité vocale des Perdrix augmente à l'aube et au crépuscule (Pépin & Fouquet, 1992). Les points ont été répartis en itinéraires de 14 à 17 points, et les itinéraires ont été réalisés dans un sens puis dans l'autre pour éviter des biais horaires lors des passages. Sur chaque point, l'heure, la date, et la présence des espèces ont été relevés. Pour chacun des trois chants diffusés, la réponse territoriale (0 / 1), le délai de réponse (en secondes), et le type de réponse

(vocale, approche, approche volée, ou toute combinaison de ces différents comportements) ont été notés. Les individus ont également été localisés sur un plan de terrain, puis l'ensemble de ces informations a été consigné *a posteriori* sur un Système d'Informations Géographiques (SIG) (Quantum GIS Development Team, 2017).

3. Suivis GPS de Perdrix grises

Deux protocoles de suivis GPS ont été développés entre 2015 et 2018 sur la ZAPVS. Un premier protocole a été mis en place sur les Associations Communales de Chasse Agréées (ci-après nommées ACCA) des communes de Fors, Mougon et Prahecq en 2015 et 2016. Nous avons saisi l'opportunité d'équiper de GPS les oiseaux lâchés par les chasseurs sous forme de lâchers d'été, avant la saison de chasse. Les suivis ont été réalisés entre fin Août – début septembre (date des lâchers) et jusqu'à mi-Novembre (fin de la saison de chasse). Environ 60 Perdrix grises préalablement mesurées (masse, longueur de l'aile pliée, longueur du tarse), sexées, et équipées de GPS CatLog-S2 (Catnip Technologies Ltd, Hong Kong) ont été lâchées par commune et par an, par groupes de 15 à 20 oiseaux. Plusieurs méthodes de lâcher ont été utilisées, selon les pratiques locales des ACCA. Sur les communes de Fors et Mougon, les oiseaux étaient maintenus en acclimatation pendant 7 à 10 jours sous cages (ou parcs) de pré-lâcher (d'environ 5 m²). Soit tous les individus étaient lâchés simultanément en fin d'acclimatation, soit séquentiellement (souvent à raison de deux oiseaux par jour, afin que les individus restant sous parc rappellent les individus libérés pour sédentariser le groupe). Sur la commune de Prahecq, les oiseaux étaient lâchés directement (sans phase d'acclimatation), et des individus appelants (mâles chanteurs mis dans des cages individuelles) étaient laissés sur site pendant 1 – 2 jours pour sédentariser le groupe lâché. Une étroite collaboration avec les chasseurs a permis de récupérer les GPS (et les données stockées) sur les Perdrix prélevées, ainsi que les GPS retrouvés sur des carcasses lors de la chasse.

Un second protocole a été développé sur le territoire de l'ACCA de Marigny, sur lequel les chasseurs se sont engagés dans une suspension de 3 ans de la chasse à la Perdrix grise. 310 oiseaux ont été lâchés (mi-décembre 2016, mi-septembre 2017 et fin-octobre 2017) par groupes de 12 à 16 individus (50% mâles et 50% femelles). Tous les individus ont été mesurés, sexés, bagués (bagues couleur et bague métal gibier à code alphanumérique) et 6 à 8 individus ont été équipés de GPS (majoritairement des CatLog-S2 ; mais également quelques GPS à transmission de données : 5 dispositifs UvA-BiTS GPS-trackers, www.uva-bits.nl, Bouten, Baaij,

Shamoun-Baranes, & Camphuysen, 2013 en 2016 voir Fig. 7; et 2 dispositifs Milsar GsmRadioTag-S9, www.milsar.com en 2018). Les oiseaux ont été placés en acclimatation sous parc de pré-lâcher (d'environ 5 m²) pendant 5 jours (3 jours lorsque des traces de prédateurs étaient observées autour des cages). Hormis ce cas particulier, tous les individus ont été lâchés à la même date, sans recourir à des individus appelants.

Dans ce second protocole, des sessions de recapture ont été réalisées afin de récupérer les GPS CatLog S2. Des cages à corvidés (30 x 40 x 30 cm) appâtées avec du blé ont été disposées auprès des sites de lâcher, des sites d'alimentation connus, et des sites où des observations récentes de Perdrix nous avaient été signalées (par des chasseurs, agriculteurs ou ornithologues). Lors des recaptures un check-up complet des individus a été réalisé : reprise des mesures faites lors des lâchers, tests de personnalité (distance de fuite, débattement en main, cris de détresse en main, perte de plumes, immobilité tonique, cris d'alarme et distance d'envol une fois relâchés), des analyses immunologiques (pour étudier l'état de santé des individus par identification et dénombrement des différents types de globules blancs), et des photographies des individus (pour obtenir la coloration de la tâche oculaire, comme mesure de l'état de santé des individus).



Figure 7 Photographie d'un mâle de Perdrix grise issu d'élevage, équipé d'un GPS (UvA-BiTS GPS-trackers, www.uva-bits.nl, Bouten et al., 2013), lâché sur la commune de Marigny (Deux-Sèvres, Nouvelle-Aquitaine) en décembre 2016.

Chapitre I

*Changement des patrons de sélection de
l'habitat chez la Perdrix grise en relation avec
la dynamique du paysage agricole au cours des
20 dernières années*

(Publié dans Ecology and Evolution)

Avant-propos et résumé du Chapitre I

Depuis une vingtaine d'années, la relation de cause à effet entre l'intensification des pratiques agricoles et le déclin des populations d'oiseaux a été mise en évidence à plusieurs reprises et est maintenant reconnue. Plusieurs études se sont accumulées démontrant les effets de l'intensification des pratiques agricoles sur la diminution de la qualité d'habitat et de la ressource alimentaire pour les oiseaux. Cependant, la réponse des oiseaux en termes de préférences d'habitat à ces changements paysagers reste très peu documentée, bien qu'elle soit primordiale pour la gestion et la conservation des populations.

Dans ce chapitre, à partir d'observations de Perdrix grises collectées sur le long terme (1997-2017), nous avons modélisé la relation entre occurrence de Perdrix grise et paysage agricole en intensification le long de 17 fenêtres glissantes de 5 ans. Plus particulièrement, nous avons évalué l'importance des éléments paysagers sur l'occurrence de la Perdrix grise (via l'analyse des contributions des variables), la relation à ces éléments paysagers, et la dynamique de la qualité d'habitat compte-tenu de ses préférences.

Nos résultats montrent un changement des préférences d'habitat au cours du temps, qui suggèrent un évitement moins prononcé des éléments paysagers associés à un fort risque de prédation par les carnivores (boisements, zones bâties) et une sélectivité croissante des infrastructures humaines (routes et chemins). Dans le même temps, une perte de surface de 26% des patchs d'habitats favorables pour l'espèce a été détectée.

La Perdrix grise ne semble pas avoir ajusté sa sélection de l'habitat de manière adéquate pour faire face à la dynamique des paysages agricoles. La diminution continue de la densité de population appuie cette conclusion. Nous soulignons l'importance de réallouer les efforts vers une amélioration de la qualité de l'habitat (couverts refuges, insectes, graines), une gestion cynégétique assurant le maintien de populations viables, et le lâcher d'oiseaux de qualité (sauvages, sensibilisés au risque par entraînement anti-prédateur). Le recouvrement de cette espèce passe nécessairement par une gestion territorialisée et intégrée, impliquant chasseurs, agriculteurs, gestionnaires et scientifiques.

**Changes in habitat selection patterns of the grey partridge *Perdix perdix*
in relation to agricultural landscape dynamics over the past two decades**

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Abstract

1. Changes in agricultural practices have reshaped agricultural landscapes and triggered a drastic decline in spatial and temporal heterogeneity leading to changes in habitat quality and food resources for birds. However the precise relationships between landscape changes, spatial and temporal heterogeneity, and habitat preferences in response to those changes, remain poorly known.
2. We investigated patterns of habitat selection and causes for changes over the years 1997-2017 for the grey partridge *Perdix perdix*, an iconic farmland species which has experienced a severe decline since the 1950's. Using a long-term (1997-2017) dataset collected over 435 km², we modeled relationships between annual land-cover maps and partridge sightings over 17 five-year moving windows, assessing the effects of landscape metrics, the strength of the relationships, and the dynamics of habitat suitability.
3. We detected a shift in grey partridge habitat preferences over time, toward more risky habitats. Avoidance of predator reservoirs (woodlands and buildings) has weakened

and selection of human infrastructure, such as roads and tracks, has increased. Since 1997, the mean size of suitable patches has also decreased by about 26%.

4. We have interpreted these changes in habitat selection as being the result of decreasing habitat quality and the increasing prevalence of captive-reared birds, currently released in their thousands in the study site.
5. *Synthesis and applications.* The grey partridge has not adjusted well to changes in farming practices and the low, still decreasing, population density suggests that it is not sustainable, despite local initiatives and the investment in captive-bird releases. We emphasize that efforts must be redirected towards habitat improvement to restore the density of refuge cover, insects and seeds in the landscape, hunting management to ensure self-sustainable populations and massive releases of high-quality birds. Only integrated local management, involving hunters, farmers, gamekeepers and scientists can ensure the recovery of this species.

Key words

Agricultural landscapes, Farmland birds, Grey partridge, Habitat quality, Habitat selection, Habitat suitability maps, Long-term trends, *Perdix perdix*.

Introduction

For decades, evidence has accumulated that the main driver of the decline in farmland biodiversity lies in the rapid post-war changes in agricultural practices (Benton, Vickery, & Wilson, 2003; Krebs, Wilson, Bradbury, & Siriwardena, 1999; Robinson & Sutherland, 2002). Agricultural intensification and specialization have reshaped and simplified agricultural landscapes (Benton et al., 2003). The resulting loss of spatial and temporal heterogeneity has degraded habitat quality and food resources, resulting in severe declines in European farmland birds (Benton et al., 2003; Chamberlain, Fuller, Bunce, Duckworth, & Shrubbs, 2000; Robinson & Sutherland, 2002). Though agricultural landscapes cover about 40% of the earth's terrestrial biomes, and are highly dynamic, long-term changes in agricultural landscapes have seldom been quantified: only seven (3%) in a review of 244 studies assessing land-cover changes (Uuemaa, Mander, & Marja, 2013). The scarcity in such studies comes from the challenge of accessing land-cover data over the long term (Bertrand, Burel, & Baudry, 2016) as well as the complexity of analyzing interacting landscape features, each with their own spatio-temporal dynamics. For instance, in intensive agricultural landscapes, buildings, roads, hedgerows and woodlands have broadly remained stable over the years, while crops change annually in a quasi-stochastic spatial pattern of crop rotation (Bretagnolle et al., 2018b). As a result, very few studies have investigated the temporal changes in habitat selection by farmland birds associated with the temporal changes in the agricultural landscape (but see Brambilla et al., 2010), despite the behavioral process of habitat selection being critical in determining population dynamics, survival, and productivity (Jones, 2001).

The grey partridge *Perdix perdix* L. used to be one of the most common farmland birds in Europe, but has been in a steep, widespread decline since the mid-20th century (Aebischer & Potts, 1994; Gée, Sarasa, & Pays, 2018; Sotherton, Aebischer, & Ewald, 2014). In many European countries, numbers are at less than 10% of their pre-war level (Aebischer & Kavanagh, 1997). For example, the drop in abundance was estimated at 92% between 1970 and 2015 in the UK, and it is now a red-listed species in the UK Birds of Conservation Concern (Hayhow et al., 2017). Despite a decline of 23% in abundance from 1989 to 2015 (Vigie-Nature, 2018) and 20% in the distribution range from 1985 to 2013 (Comolet-Tirman et al., 2015), grey partridge is still considered as 'Least Concern' in France. The decline was attributed to three main causes, all linked to the decrease in habitat quality resulting from agricultural intensification: the loss of breeding habitat, the decrease in availability of insects for chicks,

and the concentration of partridges and predation pressure in remaining habitats (Aebischer & Ewald, 2012). Grey partridge habitat selection has been well studied: at a large scale, the species avoids woodlands, associated with high predation risk, as woodlands are predator reservoirs (Dudzinski, 1992), and also avoids the proximity of buildings with their predation risks from cats and mustelids (Reitz, Le Goff, & Fuzeau, 2002). At a more local scale, during the breeding season, grey partridges were found to be attracted by cereal cover, with a high nesting success rate, (Bro, Reitz, & Mayot, 1998; Bro et al., 2013), rape and grassy covers (Birkan, Serre, Skibniewski, & Pelard, 1992; Bro et al., 2013), crop diversity (Reitz et al., 2002) and linear features such as hedgerow fragments, roads and tracks (Blank, Southwood, & Cross, 1967; Bro et al., 2013; Potts & Aebischer, 1991), even though these linear features are associated with lower nesting success (Bro et al., 1998). However, with a few exceptions (Reitz et al., 2002; Ronnenberg, Strauß, & Siebert, 2016), in most studies, the effects of landscape features have been studied independently from each other so that the relative contributions of different landscape features on grey partridge habitat selection remain unknown. Even less is known about potential changes in patterns of habitat selection over time in highly dynamic agricultural landscapes.

Here we investigated long-term trends in grey partridge habitat preferences in a French farmland landscape, through a multi-step approach using data collected annually in an area of 435 km² over 21 years (from 1997 to 2017). We first identified the key landscape features that explain the grey partridge occurrence over 1997-2017 studying the variable contributions to the probability of occurrence. Contributions reflect the importance of variables to explain (or predict) the occurrence of a species, and are commonly used to identify the key drivers of species distribution (e.g. Bellard, Leroy, Thuiller, Rysman, & Courchamp, 2016; Wilson, Sexton, Jobe, & Haddad, 2013). Secondly, to explore whether and how the habitat selection patterns have varied with changes in the landscape, we quantified changes in the relative contributions and effect of landscape features on grey partridge occurrence with time, over 17 five-year moving windows. Thirdly, we investigated whether overall habitat suitability for grey partridge has changed over time, using as reference the oldest habitat preferences of grey partridge available (i.e. models based on data from 1997-2001) (see Pearman, Guisan, Broennimann, & Randin, 2008). In this study area, significant changes in land-cover, for example a 20% increase in cereal cover since 1994 (Bretagnolle et al., 2018b), and a decrease in insect availability (Bretagnolle et al., 2011) have been recorded while observed partridge densities have strongly

decreased (Fig. 1b) despite huge annual releases of captive-reared birds to maintain local partridge populations (Bro & Crosnier, 2012). Given this observed decline in the study population associated with the relatively stable amount of captive-reared grey partridges annually released in France from 1995 to 2015 (around 2 million individuals in Bro, 2016), we therefore, assumed that the population in our study area has changed from mainly wild birds in the nineties to mainly released captive-reared birds currently. We thus suggested the massive releases of captive-reared birds as a potential driver of changes in the pattern of habitat preferences. Indeed, we might expect that naïve partridges would be less likely to avoid predator-rich habitats. If there has been a general decline in habitat quality, partridges may select the least altered or highest quality habitats. Although habitat selection is density dependent (Morris, 1989), over the same period the population of partridges has strongly declined, so that habitat preferences may have remained targeted to the highest quality habitats.

Material & methods

Study site and environmental layers

The Long-Term Socio-Ecological Research platform (LTSER) “Zone Atelier Plaine & Val de Sèvre” is located in Central Western France, Nouvelle-Aquitaine region (Fig. 1a, Bretagnolle et al., 2018b). This area is characterized by an intensive agricultural landscape for cereal production. Land-cover has been exhaustively surveyed annually from 1994 onwards using more than 40 crop categories. Winter cereals largely dominate (41.5%, mean value calculated over the years 2009 to 2016), followed by sunflower (10.4%), maize (9.6%), rape (8.3%) and meadows (13.5%). Woodland fragments represent 2.9% of the study area (excluding the Chizé forest), and built-up areas (including isolated buildings), 9.8%. A preliminary analysis of landscape features showed that the density of hedgerows, buildings and woodlands have varied little whereas the areas of cereals, meadows and rape, as well as crop diversity and the size of crop patches have changed far more over the period (Fig. 1c-d, Fig. S1 and Table S1 for statistical details). In addition, crop locations change annually because of crop rotation.

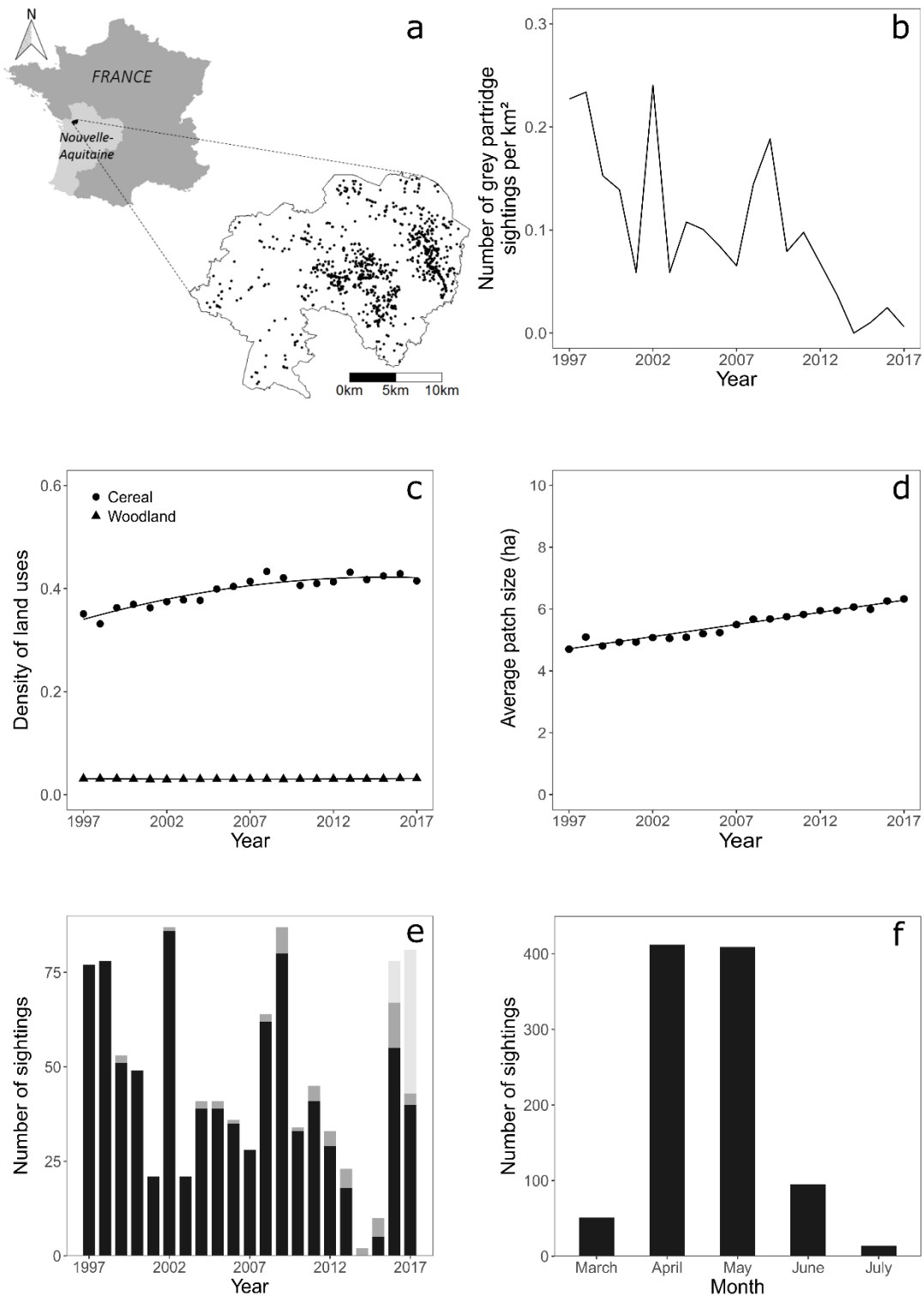


Figure 1 (a) Location of the Long-Term Socio-Ecological Research (LTSE) platform "Zone Atelier Plaine & Val de Sèvre" in France. Black dots inside the LTSE represent grey partridge sightings recorded from 1997 to 2017. (b) Density of grey partridge opportunistic sightings (see Methods), from 1997 to 2017. (c) Density of cereals (time varying) and woodland (stable) from 1997 to 2017. Solid lines represent significant trends from generalized least squares (GLS) model with autoregressive moving average (see Table S1 for statistical details). (d) Average size of crop patches from 1997 to 2017 on the LTSE. Solid lines represent significant trends from GLS models with autoregressive moving average. (e) Grey partridge sightings each year between 1997 and 2017 for each dataset (black: opportunistic sightings; dark grey: point counts; light grey: point counts with call playback). (f) Distribution of grey partridge sightings recorded in each month of the year from 1997 to 2017.

The vector based GIS was first transformed into a grid of 200*200 m² cells (4 ha), using R (R Core Team, 2017) and QGIS (Quantum GIS Development Team, 2017), excluding all pixels that had less than half their area intersecting with the study area. The pixel size was chosen to have a meaningful fine scale resolution in relation to landscape dynamics that was close to the average field size (Bretagnolle et al., 2018b). Landscape features already identified in the literature as being selected by grey partridges were chosen for analyses as potential predictors of the grey partridge occurrence: cereals, rape, meadows, hedgerows, roads and tracks (Birkan et al., 1992; Blank et al., 1967; Bro et al., 2013), and woodland and buildings, features that partridges avoid (Dudzinski, 1992; Reitz et al., 2002). The landscape metrics (i.e. layers assessing landscape features) used in the analyses comprised the densities of various landscape features (the area in ha, or length in meters, of each landscape feature divided by area of the pixel in ha), the crop diversity (Shannon-Wiener diversity index calculated for five main crops (cereals, rape, meadow, maize, and sunflower), and “other crops”), the mean size of the crop patches (mean area of the patches of the main crops intersecting each pixel), and the distances from features avoided by partridges (distances from the center of the pixel to the closest woodland and closest building) (Table S2). Each of these seven metrics was calculated for each of the 21 years from 1997 to 2017 giving 147 map layers. Roads, tracks, and hedgerows have remained fairly stable over the period (Appendix A, Fig. S1) so one map layer was used for roads and tracks and three layers for hedgerows in 2006, 2011 and 2014 when aerial photographs were available. A total of 151 layers were, therefore, included.

Partridge data

In total, there were 989 sightings of grey partridges in three distinct datasets covering 1997 to 2017 (Fig. 1e). The largest dataset (90% of total data), comprised opportunistic sightings either when ornithologists working in the LTSEr were studying other bird species (Bretagnolle et al., 2018b) and saw partridges, or during the land-cover surveys carried out twice a year systematically over the entire study site. Each year, opportunistic sightings were reported daily between late March and late July (see Fig. 1f). In this dataset, the observation effort is not standardized and reporting is not systematic. In the second dataset, with 5% of total sightings, observation pressure is standardized as this dataset collates the results from systematic bird point counts since 1995 (see Brodier, Augiron, Cornulier, & Bretagnolle, 2014 for methods). The number of point counts has increased from 160 (1995-2008) to about 450

since 2009, spread over the whole of the LTSE (Bretagnolle et al., 2018a). Count duration was either 5 or 10 minutes (see Brodier et al., 2014) between 7:00 am to 11:00 am, without call playback. The third dataset, with 5% of total sightings, collates the results of standardized call playback counts specifically for both grey partridges and red-legged partridges *Alectoris rufa* L., in March-April 2016 (140 sites) and 2017 (275 sites), either in the morning (from 7:00 am to 11:00 am) or evening (from 5:00 pm to 9:00 pm). Count duration was 10 min. In all three datasets, the location of the birds, the date and time, and the number of birds were recorded. We restricted our analyses to data collected during the breeding season, from late March until July (Fig. 1f), using the data in all three datasets.

Species distribution models

A multi-step approach using species distribution modeling was carried out to (1) identify key landscape features and their effect on the grey partridge occurrence over the entire period 1997-2017; (2) explore trends in the contribution of key features and in their effect over 17 successive 5-year moving periods; (3) assess changes in habitat suitability for grey partridge over time.

Modeling process

The following modeling process was first applied over the entire study period (1997-2017) to investigate the general pattern of habitat selection. Each landscape metric was pooled over the entire study period 1997-2017 (calculating an average value by pixel). To perform the trend analysis assessing changes in habitat selection patterns, the modeling process was also applied using a five-year moving window, giving 17 successive 5-year periods from 1997-2001 to 2013-2017, to have between 100 and 300 sightings at each time step (see Barbet-Massin, Jiguet, Albert, & Thuiller, 2012). Each landscape metric was thus also pooled by 5-year periods.

We began by selecting uncorrelated landscape metrics to ensure the validity of the predictions (Barbet-Massin & Jetz, 2014) using the method described by Leroy et al. (2013), resulting in nine uncorrelated explanatory variables for the dataset with 5-year moving windows (Table S2), however the rape density was excluded for modeling the dataset aggregated over the whole period (Appendix B). Secondly, to select the modeling technique (Elith, Ferrier, Huettmann, & Leathwick, 2005), we used version 2.0 BIOMOD multi-model platform (Thuiller, Lafourcade, Engler, & Araújo, 2009) implemented in R. This can (1) use

heterogeneous data from different counting methods (Farashi & Shariati, 2017; Jackson, Gergel, & Martin, 2015) and (2) compare the most frequently used modeling techniques (Barbet-Massin et al., 2012; Monnet, Hingrat, & Jiguet, 2015) (see Appendix C). As these modeling techniques require presence and absence data but as our dataset did not contain true absences (the absence of a sighting does not imply the absence of partridges), we generated 100 replicates of 1000 random pseudo-absences to obtain reliable confidence intervals (Barbet-Massin et al., 2012) (Appendix C gives the methods and numbers of pseudo-absences). Generalized linear models (GLM, binomial response variable, logit link) were selected for the rest of the analyses as they showed a high true skill statistic (TSS = sensitivity + specificity - 1) (Allouche, Tsoar, & Kadmon, 2006) and high sensitivity (Appendix C). For each period, the models were calibrated on a random subset of 70% of the presence / pseudo-absence data, and then cross-validated using the remaining 30%: this cross-validation was performed three times (Thuiller, Lafourcade, & Araujo, 2009). The TSS was used to evaluate the predictive performance: TSS ranges from -1 to 1, where 1 represents perfect agreement while scores ≤ 0 represent a performance no better than random (Allouche et al., 2006). For each period, the mean TSS was calculated averaging each model's TSS. The final calibration of each model used 100% of the available data.

Assessing the contribution of each landscape metric

The average contribution of each landscape metric on the probability of the occurrence of grey partridge was determined for the entire period 1997-2017, and for each of the successive 5-year periods using the *biomod2 variables importance* function. First, a standard prediction of grey partridge probability of occurrence is made across all pixels of the study area from a model calibrated with all explanatory variables. Then, the values of a given variable are randomly permuted across pixels and a new prediction is made. The contribution of the given variable to the prediction of the probability of occurrence is 1 less the correlation between the standard and the random predictions: the higher the correlation, the weaker the contribution or predictive power of the variable to explain the species occurrence (Leroy et al., 2013). Ten randomizations were used for each variable with a threshold of 0.1 to distinguish between strong and weak contributions (Leroy et al., 2013) which corresponded to the mean importance for all variables (Capinha & Anastácio, 2010).

Effect of landscape metrics on the grey partridge occurrence

The relationship between landscape metrics and the probability of the occurrence of grey partridge was assessed using the average response curves from GLMs calibrated on 100% of the data. The 95% confidence intervals were calculated as a measure of the uncertainty for 100 GLM runs. The range of habitat values selected by partridges were drawn based on the average cutoff calculated for each period (Wilfried Thuiller, pers. comm., 2016). The cutoff is the threshold maximizing TSS and is calculated for each model run under *biomod2* (Leroy et al., 2013; Wilfried Thuiller, pers. comm., 2016).

Trends in the relation between partridge occurrence and landscape metrics

To test whether time (explanatory variable) had a significant effect on the contribution (response variable) of landscape metrics, we used a generalized least squares (GLS) model using the *nlme* package. To handle autocorrelation in our time series, we run an autocorrelation function on each dependent variable to identify the time lag after which the non-autocorrelation assumption was confirmed at 95% confidence level (Shumway & Stoffer, 2011). Then GLSs were implemented with an autoregressive moving average (ARMA) term in which the moving average (MA) errors were accounted for using the maximum time lag determined in the previous step. The lack of sequential autocorrelation in the residuals was checked using the *acf* function. The 5-year moving average windows allow a smoothing effect in the shape of the relationship between time and variable contribution. Finally, we included a quadratic time term in the GLS models and used backward stepwise selection procedure (Faraway, 2005).

The curves for each of four contiguous windows (1997-2001, 2002-2006, 2007-2011 and 2012-2016) were also drawn for each landscape metric that both made a large contribution and changed significantly with time.

Habitat suitability maps and trends in habitat quality

We forecasted habitat suitability maps for the periods 1998-2002 to 2013-2017 from the models fitted to the period 1997-2001 to assess how suitable habitats formerly selected by partridges have shifted over time. Habitat suitability was mapped as the probability of occurrence from an ensemble model, averaging all GLMs with TSS > 0.4 (Engler et al., 2011; Zhang et al., 2015), each one weighted by its TSS. Then, we calculated Schoener's D (Schoener,

1968 reviewed by Warren, Glor, Turelli, & Funk, 2008) as a measure of similarity in the geographical space between the habitat suitability maps of each period and the earliest one (1997-2001).

$$D(p_X, p_Y) = 1 - \frac{1}{2} \sum_i |p_{X,i} - p_{Y,i}|$$

where $p_{X,i}$ and $p_{Y,i}$ represent the probabilities of occurrence of the grey partridge in the pixel i for the periods X and Y . The maps were then transformed into binary maps of suitable *versus* unsuitable areas, the threshold being the cutoff of the models calibrated on data of 1997-2001 (Leroy et al., 2013). The averaged value of habitat suitability index (i.e. the probability of occurrence) and the mean size of suitable habitat patches were calculated for each period.

Results

First, we investigated the key landscape metrics explaining the grey partridge occurrence over the study period (1997-2017), and their effect on grey partridge occurrence. Of the nine candidate explanatory variables, cereal density, distance to woodlands and distance to the nearest building were the metrics with the highest contributions when fitting to the aggregated dataset for 1997-2017 (contributions >0.1 , Fig. 2; Table S3). Most response curves were quadratic: moderate values of cereal density (25% to 65%) and distance to woodlands (300 m to 1310 m) were preferred by partridges while extreme values were avoided (Fig. 3). Partridges also preferred being more than 125 m from a building (Fig. 3).

For the contiguous five-year periods, most of the metrics had similar contributions to those for the whole dataset (Fig. 2; compare black and grey boxes), though the contribution of the distance to buildings was below the 0.1 threshold and the contribution of the road density increased above the 0.1 threshold (Fig. 2). The response curve for road density was also quadratic with a preference for densities between 20 m/ha and 200 m/ha (high road densities were mainly in built-up areas) (Fig. 3).

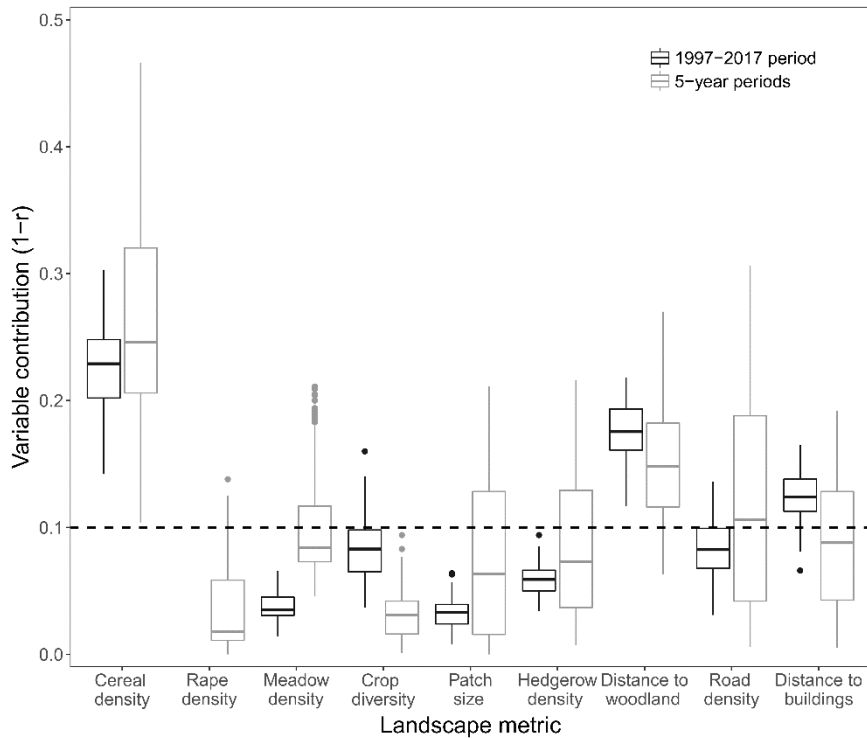
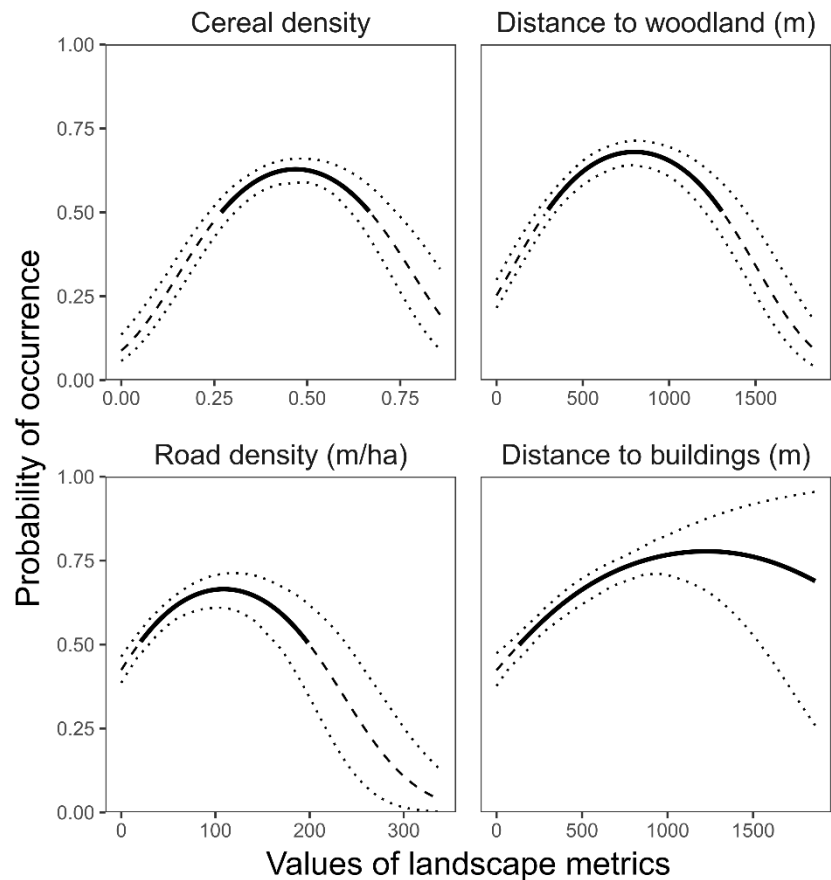


Figure 2 Contributions of landscape metrics to models calibrated on the whole 21-year period (black) and cumulative contributions to models calibrated on the four contiguous five-year periods (1997-2001, 2002-2006, 2007-2011, 2012-2016). Rape density was discarded from the analysis for the whole 21-year period as it was correlated with cereal density. The dashed line represents the threshold used to distinguish the landscape metrics that contributed most to the model (Capinha & Anastácio, 2010; Leroy et al., 2013).

Figure 3 Probability of occurrence of grey partridge as a function of the landscape metrics that contributed most. Dashed lines represent the mean probability of occurrence below the cutoff, dotted lines represent 95% confidence intervals, solid lines represent the range of values selected by grey partridge (above the cutoff, see Methods).



Then, we performed a trend analysis to investigate whether the importance of the key landscape metrics and their effect on grey partridge occurrence have changed with time. The trend analysis of the 17 five-year moving windows showed that there were significant variations over time in the contributions of some metrics (Table S4). For example the contribution of cereal density was variable in the first few years and then increased in the last 15 years. This increase in contribution was associated with a decrease of sightings in areas with low cereal density unselected by partridges (13% of sightings in area with cereal density < 0.25 in 1997-2001; 7% in 2012-2016; Table S5). The contribution of road density increased over the whole period with the selected range contracting from 0-270 m/ha in 1997-2001 to 35-165 m/ha in 2012-2016 (Fig. 4, Table S6). Recently partridges appeared to avoid woodlands and to buildings less, as the contributions of these metrics decreased (Fig. 4, Table S4). Currently, partridges prefer areas closer to woodlands (distance to woodlands is 19.5% shorter) than at the start of the study period (820 m in 1997-2001 decreasing to 660 m in 2012-2016, Fig. 4, Table S6). This result is also consistent with raw numbers of partridge sightings (15% of sightings at a distance to woodlands < 250 m in 1997-2001; 22% in 2012-2016; Table S5). Partridges were less likely to avoid buildings in recent years than in 1997-2001 when they avoided areas closer than 160 m to a building (Fig. 4, Table S6). In 1997-2001, 13% of sightings were collected at a distance lower than 160 m to buildings, against 21% in 2012-2016 (Table S5). The contribution of the size of crop patches decreased while that of hedgerow density increased, but both contributions were small (Fig. S2, Table S4).

Finally, we assessed the trends in habitat suitability with time. Habitat suitability maps calibrated on the first period (1997-2001) and forecast using the 1998-2002 to 2013-2017 metrics, suggested a general decrease by about 26% in the mean size (from 26.4 ha in 1997-2001 to 19.6 ha in 2013-2017) and a slight decrease in the mean suitability index (from 0.696 in 1997-2001 to 0.682 in 2013-2017) of suitable patches for partridges (Fig. 5). Schoener's D statistic assessing the similarity of the habitat suitability maps between each 5-year period and the first one decreased by 18.5% over time (Fig. 5, Table S7). Even though the quality of our models remained relatively low (TSS= 0.42 ± 0.03 for the seventeen 5-year periods, Table S3), it was high enough to be considered useful being above the recognized threshold of 0.4 (Engler et al., 2011; Zhang et al., 2015).

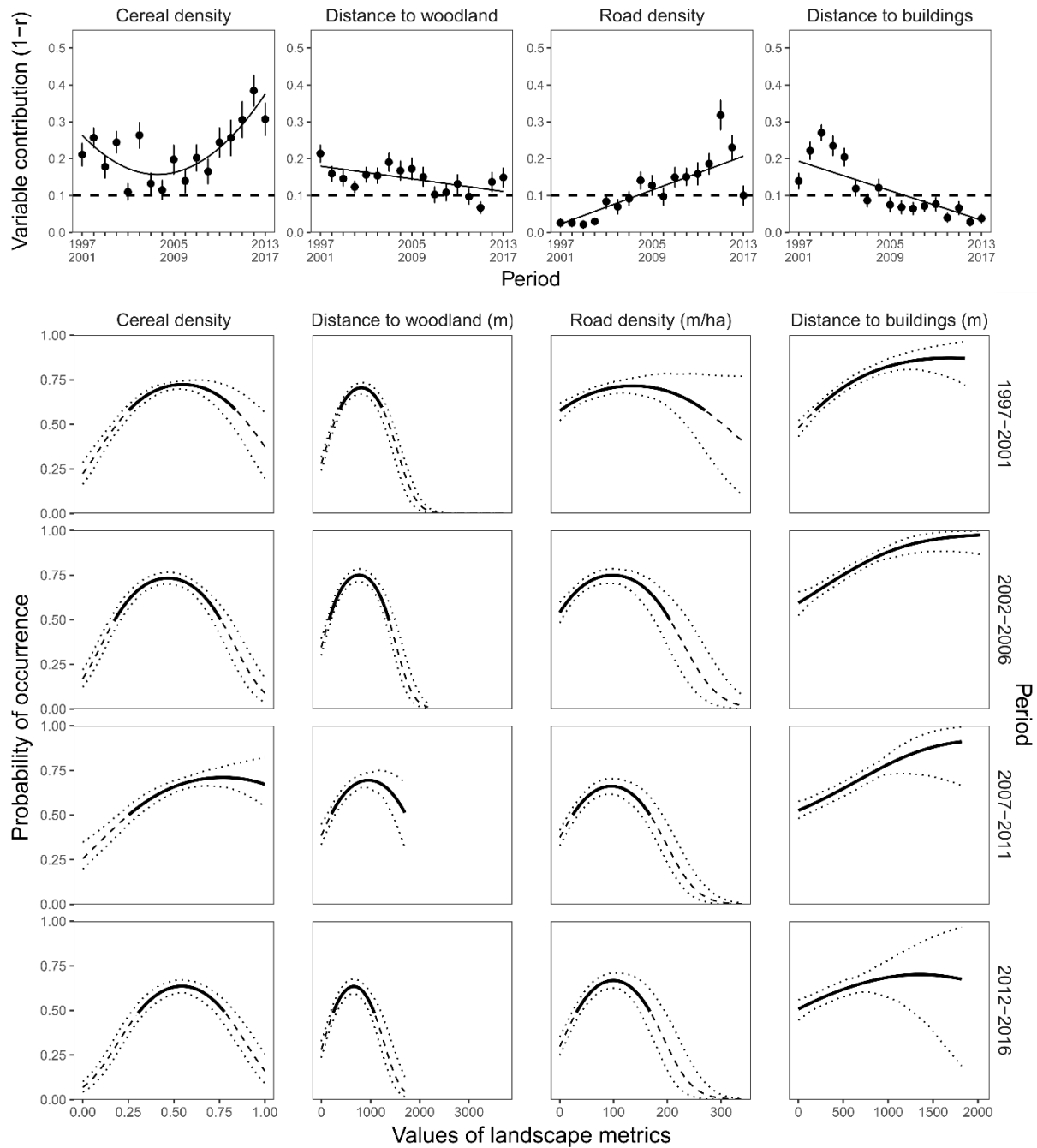


Figure 4 Top: contributions (black dots) of landscape metrics in the 5-year moving window. Solid lines show the trends from the GLS model with autoregressive moving average (see Table S4 for statistical details). The dashed line represents the threshold used to distinguish the landscape metrics that contributed most to the models (Capinha & Anastácio, 2010; Leroy et al., 2013). Error bars correspond to the standard deviation of the contributions. Bottom: Probability of occurrence of grey partridge as a function of the landscape metrics for the four contiguous five-year periods (1997-2001, 2002-2006, 2007-2011, 2012-2016). Dashed lines represent the mean probability of occurrence below the cutoff, dotted lines represent 95% confidence intervals, solid lines represent the range of values selected by grey partridge (above the cutoff, see Methods).

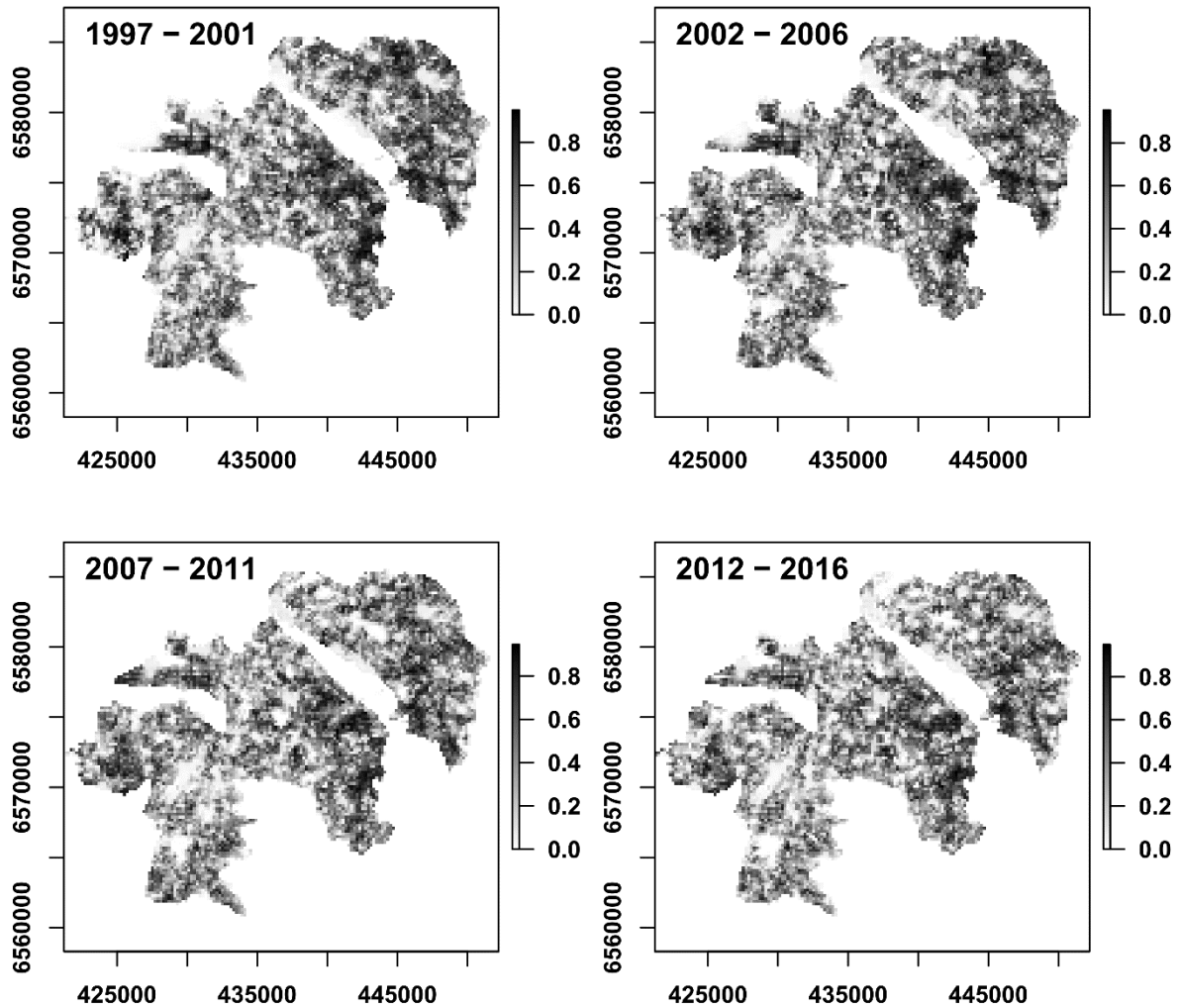


Figure 5 Predicted habitat suitability index of the LTSE for the four five-year contiguous periods. X and Y axes are the coordinates (Lambert 93, EPSG: 2154).

Discussion

Despite many releases of captive-reared birds in the study area, the population of grey partridges has suffered a drastic decline over the last 21 years. While we observed a general decrease in the size and suitability index of suitable patches, our study showed that occurrence of partridges has changed with landscape features.

Considering the overall 21-year period (1997-2017), the density of cereals, the distance to woodlands and the distance to the nearest building were identified as the main contributors or key drivers of grey partridge occurrence (Bellard et al., 2016; Wilson et al., 2013). Cereals is well known as the main breeding cover selected by grey partridges (69 % of nests in Bro et al., 2013), associated with high nesting success (Bro et al., 1998). However, the response curve shows saturation, indicating a need for complementary habitats, for example rape for food

(Birkan et al., 1992). High contributions of distances to woodlands and buildings were expected because of avoidance of carnivore reservoirs (Dudzinski, 1992; Reitz et al., 2002; Reitz & Mayot, 1999) and woodlands have already been identified as the main driver of grey partridge distribution at local district scale (Ronnenberg et al., 2016). For the four five-year contiguous periods the distance to buildings was less important while road density was more important. Partridges avoided low road densities, as nesting sites are frequently close to roads (25% of nests located in cereals, Bro et al., 2013), but they also avoided high road densities, either because of predation risk (Reitz & Mayot, 1999) or disturbance by traffic (Fahrig & Rytwinski, 2009). Although the population was mainly captive bred, this suggests that the partridges showed patterns of habitat selection that were driven by well-known ecological requirements.

An unexpected result is that there was a strong increase in the contribution of cereals to explain the grey partridge occurrence over the past 15 years. As the cereal density has increased by about 20% of the preexisting density observed in 1997 (Bretagnolle et al., 2018b), this cover has become more widespread, and a subsequent decrease in the contribution of cereals might be expected. The selection and high nesting success of cereals (Bro et al., 2013, 1998), associated with the depletion of grey partridge densities may explain this result. The depletion would have been higher in the low and unselected densities, as supported by the decreasing number of sightings in areas providing low cereal densities. The other main result is the decreasing contributions of distances to woodlands, buildings, on the partridge occurrence, associated with increasing proportions of partridge sightings close to these predator-rich features. While these landscape features have remained fairly stable over time, this suggest that partridges became less likely to avoid woodlands and buildings (predator reservoirs) and roads (high exposure to predation) (Reitz & Mayot, 1999), though they were expected to select the best quality habitats. Nonetheless, lower avoidance of roads could also be partly explained by the decreasing partridge density associated with the opportunistic nature of sightings, usually collected from roads. Such shifts in grey partridge habitat preferences towards more risky habitats associated with lower survival expectancy have already been described and explained by captive rearing of partridge and other galliformes, lacking antipredator behavior (Rantanen, Buner, Riordan, Sotherton, & Macdonald, 2010a, 2010b; Sokos, Birtsas, & Tsachalidis, 2008). Furthermore, captive-reared birds could also suffer from natal habitat preference induction (Stamps & Swaisgood, 2007), encouraging them

to select anthropogenic features similar to those where they were reared. However, as habitat selection impairing fitness has also been documented in wild grey partridges (Bro, Mayot, Corda, & Reitz, 2004) and other farmland birds (e.g. the yellow wagtail *Motacilla flava* in Gilroy, Anderson, Vickery, Grice, & Sutherland, 2011), there may be another explanation. This shift in habitat selection pattern could be linked to a behavioral adjustment to the decreasing habitat quality and food availability. For instance, over the last 30 years, seed availability has dropped faster in field cores than at field edges (Fried, Petit, Dessaint, & Reboud, 2009). Partridges could, therefore avoid roads less, as roadside habitats may provide more insect and seed food (Hopwood, 2008; von der Lippe, Bullock, Kowarik, Knopp, & Wichmann, 2013) and higher seed abundance has already been linked to higher densities of farmland birds, including grey partridge (Moorcroft, Whittingham, Bradbury, & Wilson, 2002). This hypothesis could also explain the increase in the contribution of cereal density as the decrease in landscape diversity would encourage partridges to prefer this cover which is associated with a high nesting success rate (Bro et al., 2013, 1998). The continuous drop in habitat quality caused by agricultural intensification, could have increased the concentration of prey and the predation pressure on the remaining suitable patches (Aebischer & Ewald, 2012). This raises concern about low-density populations, which may be particularly damaged as a result of a behaviorally mediated Allee effect: there is no competition for space and individuals are free to select their preferred, though possibly associated with lower survival, habitats (Kokko & Sutherland, 2001).

Implications for management

The grey partridge study population, with a current density of around 1 male (or pair) per 400 ha, may not be sustainable. Additionally, the observed changes in habitat selection towards more risky habitats could impair the situation and may be exacerbated by releases of captive-reared birds, documented to suffer deficiencies in antipredator behaviour, poor survival and breeding success (Parish & Sotherton, 2007; Rantanen et al., 2010b). Therefore, initiatives releasing captive-reared birds (about 250 birds per 1700 ha, the mean area of a local community) may actually precipitate, rather than mitigate, the fate of local populations, since these naïve birds outnumber wild individuals (Reitz, 2003; Sokos et al., 2008). Furthermore, these costly release programs, about €55k to €60k each year in the LTSER (36 hunting associations × 250 birds × €6.5), have so far failed to help the population recover, as numbers

are still declining in the LTSE and the surrounding countryside. Extrapolating to other gamebird species (€55k to €60k per year for red-legged partridges and €45k to €50k for ring-necked pheasants) the costs of supplementing the local populations of gamebirds can be estimated at €155k to €170k per year in our study area, with no perceivable improvement in population sustainability.

This does not imply that reinforcement is an invalid strategy, since several conservation programs would have sustainably increased partridge densities (Bro, 2016; Browne, Buner, & Aebischer, 2009; Buner & Aebischer, 2008). These programs, however included supplementary feeding, reestablishment of refuge covers and insect-rich habitats for chicks (set-asides, grassy strips along field edges, field divisions, game covers), and nest protection or predation control when needed to accelerate population recovery (Aebischer, 2009; Aebischer & Ewald, 2012; Bro, 2016). In our study area, money saved by reducing by half the amount of captive-reared bird released (i.e. by €80k) might be reallocated to create for example 270 ha of set-asides or wildlife covers, or a maintenance of 40 km² (i.e. 1/5 of the cereal area) of stubble fields until the end of the chick rearing period. In addition, the origin of the released birds was identified as a critical factor in success whether the aim was game management or conservation (Fischer & Lindenmayer, 2000; Griffith, Scott, Carpenter, & Reed, 1989). For instance, Sokos et al. (2008) reported a failure to re-establish a pheasant population in a release program involving 3000 captive-reared birds, while the release of 1000 wild-caught individuals succeeded.

In the case of the grey partridge, we believe that we need to change from releasing captive-reared gamebirds for 'put and take' shooting (Sokos et al., 2008), to conservation programs aiming to restore self-sustaining populations. Efforts should be redirected towards habitat improvement through selected agricultural practices, to greatly increase refuge covers, insects and seeds in the landscape, with hunting restrictions to ensuring that the bird populations are self-sustaining, coupled with releases of wild-caught or predator-trained birds (Sokos et al., 2008). Creating synergy between all stakeholders, hunters, farmers and scientists, is, however, critical to achieve such integrated, local biodiversity management.

Authors' contributions

VB set up the long-term partridge and land-cover monitoring; numerous fieldworkers supervised by VB collected the data. OP, VB, MS and CH conceived the ideas and designed

methodology; CH and OP analyzed the data; CH, OP, VB and MS wrote the manuscript. All authors contributed to the drafts and gave final approval for publication.

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Data accessibility

Partridge sightings and landscape metrics: OSF doi: 10.17605/OSF.IO/QJ237

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Supporting information

Appendix A. Supplementary figures, tables and supplementary results from models calibrated on all sightings (opportunistic observations, point counts, point counts with call playback).

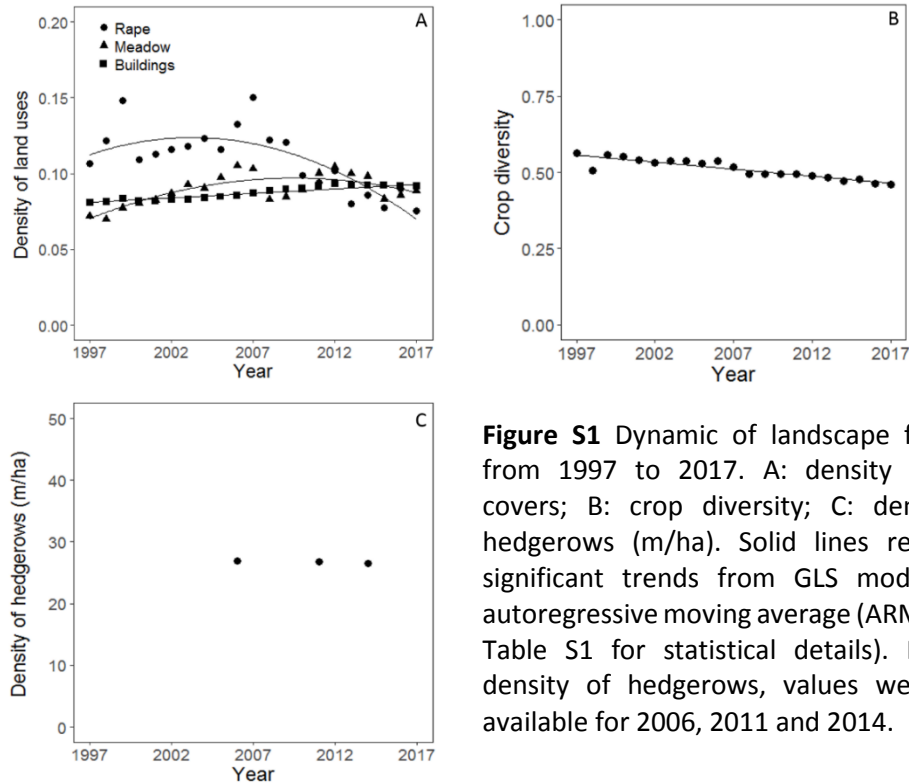


Figure S1 Dynamic of landscape features from 1997 to 2017. A: density of land covers; B: crop diversity; C: density of hedgerows (m/ha). Solid lines represent significant trends from GLS model with autoregressive moving average (ARMA) (see Table S1 for statistical details). For the density of hedgerows, values were only available for 2006, 2011 and 2014.

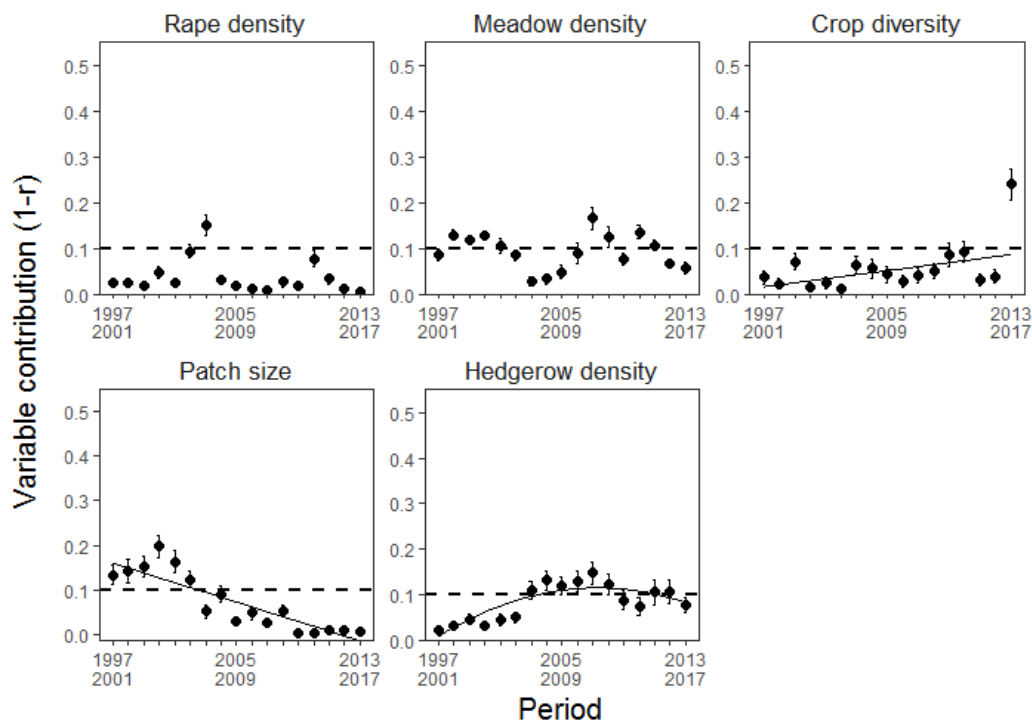


Figure S2 Contributions (black dots) of landscape metrics in 5-year moving windows from 1997-2001 to 2013-2017). Solid lines correspond to significant trends from GLS model with autoregressive moving average (ARMA) (see Table S4 for statistical details). The dashed line represents the threshold used to distinguish the landscape metrics that contributed most to the model. Error bars show the standard deviations.

Table S1 Summary of the results of the generalized least squares models with Auto Regressive Moving Average (ARMA), showing the time dependence of the landscape metrics. Significant trends are represented by solid lines in Figures S1.

Landscape metric	Type of autocorrelation	Independent variable	F value	numDf	p value	Coef ± SE
Cereal	ARMA(q=3)	(Intercept)				(0.3310 ± 0.0121)
		Time	1.864	1	<0.001	0.0095 ± 0.0025
		Time ²	5.055	1	0.037	-0.0002 ± 0.0001
Rape	ARMA(q=2)	(Intercept)				(0.1086 ± 0.0135)
		Time	9.167	1	0.007	0.0042 ± 0.0028
		Time ²	5.255	1	0.034	-0.0003 ± 0.0001
Meadow	ARMA(q=1)	(Intercept)				(0.0659 ± 0.0062)
		Time	6.389	1	0.021	0.0046 ± 0.0013
		Time ²	9.086	1	0.008	-0.0002 ± 0.0001
Crop diversity	ARMA(q=3)	(Intercept)				(0.562 ± 0.007)
		Time	64.645	1	<0.001	-0.005 ± 0.001
		Time ²	2.222	1	0.153	
Patch size	ARMA(q=4)	(Intercept)				(4.637 ± 0.088)
		Time	136.948	1	<0.001	0.079 ± 0.007
		Time ²	2.080	1	0.167	
Woodland	ARMA(q=1)	(Intercept)				(0.0314 ± 0.0003)
		Time	2.000	1	0.175	-0.0003 ± 0.0001
		Time ²	22.700	1	<0.001	0.00001 ± 0.0000
Buildings	ARMA(q=4)	(Intercept)				(0.080 ± 0.001)
		Time	57.718	1	<0.001	0.001 ± 0.000
		Time ²	0.910	1	0.353	

Table S2 Metrics used in this study, how they were obtained, the expected relationship with the probability of occurrence of grey partridge, and the underlying mechanism accounting for this effect.

Landscape metric	Calculation	Expected sign of the relationship	Underlying mechanism and reference
Cereal density	$\frac{\text{Area of cereals}}{\text{pixel area}}$	+	Nesting site selection (Bro et al., 2013)
Rape density	$\frac{\text{Area of rape}}{\text{pixel area}}$	+	Escape and food supply covers (Birkan et al., 1992)
Meadow density	$\frac{\text{Area of meadows}}{\text{pixel area}}$	+	Nesting site selection (Bro et al., 2013)
Crop diversity	Shannon Index for each pixel ($H = -\sum p_i \ln(p_i)$ with p_i the proportion of crop i in the pixel) based on the six more represented categories of crops: cereals, sunflower, maize, rape, meadow, and other crops (Bertrand et al. 2016)	+	Nesting site selection (Reitz et al., 2002)
Patch size	Cultivated fields were aggregated in six categories of crops (cereals, sunflower, maize, rape, meadow, and other crops), and then divided by roads/tracks, and the average size of the resulting patches intersecting each pixel was calculated (Bertrand et al. 2016)	-	Nesting site selection (Kaiser, 1998)
Hedgerow density	$\frac{\text{Length of hedgerows}}{\text{pixel area}}$	-	Open farmland species preferring fragmented rather than complete hedgerows (Blank et al., 1967)
Road density	$\frac{\text{Length of roads}}{\text{pixel area}}$	+	Nesting site selection near linear features (Bro et al., 2013) Seed accumulation in roadside habitats (von der Lippe et al., 2013)
		-	High road density increases the predation risk by mustelids (Reitz & Mayot, 1999)
Distance to woodland	Distance from the centre of each pixel to the closest woodland	-	Avoidance of woodlands as predator reservoirs (foxes and mustelids; Dudzinski, 1992)
Distance to buildings	Distance from the centre of each pixel to the closest building	-	Avoidance of buildings as predator reservoirs (cats, dogs, mustelids) (Putala, Turtola, & Hissa, 2001; Reitz et al., 2002)

Table S3 Mean TSS ($\pm$ sd), and mean contribution of each metric ($\pm$ sd) for each 5-year sliding window and for the whole period from 1997 to 2017. Values in bold represent TSS values above the threshold of 0.40 used to distinguish useful models and values above the threshold of 0.1 used to distinguish the metrics that contributed most to the model (Capinha & Anastácio, 2010; Leroy et al., 2013). Rape density was discarded from analyses of the whole period from 1997 to 2017 as it was correlated with cereal density.

Year	TSS	Cereal density	Rape density	Meadow density	Crop diversity	Patch size	Hedgerow density	Distance to woodland	Road density	Distance to building
1997-2001	0.44 ($\pm$ 0.05)	0.21 ($\pm$ 0.03)	0.02 ($\pm$ 0.01)	0.09 ($\pm$ 0.01)	0.04 ($\pm$ 0.01)	0.13 ($\pm$ 0.02)	0.02 ($\pm$ 0.01)	0.21 ($\pm$ 0.02)	0.03 ($\pm$ 0.01)	0.14 ($\pm$ 0.02)
1998-2002	0.47 ($\pm$ 0.04)	0.26 ($\pm$ 0.03)	0.03 ($\pm$ 0.01)	0.13 ($\pm$ 0.01)	0.02 ($\pm$ 0.01)	0.14 ($\pm$ 0.03)	0.03 ($\pm$ 0.01)	0.16 ($\pm$ 0.02)	0.03 ($\pm$ 0.01)	0.22 ($\pm$ 0.02)
1999-2003	0.44 ($\pm$ 0.05)	0.18 ($\pm$ 0.03)	0.02 ($\pm$ 0.01)	0.12 ($\pm$ 0.01)	0.07 ($\pm$ 0.02)	0.15 ($\pm$ 0.02)	0.05 ($\pm$ 0.01)	0.15 ($\pm$ 0.02)	0.02 ($\pm$ 0.01)	0.27 ($\pm$ 0.02)
2000-2004	0.46 ($\pm$ 0.05)	0.24 ($\pm$ 0.03)	0.05 ($\pm$ 0.01)	0.13 ($\pm$ 0.01)	0.01 ($\pm$ 0.01)	0.20 ($\pm$ 0.02)	0.03 ($\pm$ 0.01)	0.12 ($\pm$ 0.02)	0.03 ($\pm$ 0.01)	0.23 ($\pm$ 0.03)
2001-2005	0.45 ($\pm$ 0.05)	0.11 ($\pm$ 0.02)	0.02 ($\pm$ 0.01)	0.10 ($\pm$ 0.02)	0.02 ($\pm$ 0.01)	0.16 ($\pm$ 0.02)	0.05 ($\pm$ 0.01)	0.16 ($\pm$ 0.02)	0.08 ($\pm$ 0.02)	0.20 ($\pm$ 0.02)
2002-2006	0.45 ($\pm$ 0.05)	0.26 ($\pm$ 0.03)	0.09 ($\pm$ 0.02)	0.09 ($\pm$ 0.01)	0.01 ($\pm$ 0.01)	0.12 ($\pm$ 0.02)	0.05 ($\pm$ 0.01)	0.15 ($\pm$ 0.02)	0.07 ($\pm$ 0.02)	0.12 ($\pm$ 0.02)
2003-2007	0.44 ($\pm$ 0.05)	0.13 ($\pm$ 0.03)	0.15 ($\pm$ 0.02)	0.03 ($\pm$ 0.01)	0.06 ($\pm$ 0.02)	0.05 ($\pm$ 0.01)	0.11 ($\pm$ 0.02)	0.19 ($\pm$ 0.02)	0.09 ($\pm$ 0.02)	0.09 ($\pm$ 0.02)
2004-2008	0.42 ($\pm$ 0.05)	0.11 ($\pm$ 0.03)	0.03 ($\pm$ 0.01)	0.03 ($\pm$ 0.01)	0.06 ($\pm$ 0.02)	0.09 ($\pm$ 0.02)	0.13 ($\pm$ 0.02)	0.17 ($\pm$ 0.03)	0.14 ($\pm$ 0.02)	0.12 ($\pm$ 0.02)
2005-2009	0.37 ($\pm$ 0.05)	0.20 ($\pm$ 0.04)	0.02 ($\pm$ 0.01)	0.05 ($\pm$ 0.02)	0.04 ($\pm$ 0.02)	0.03 ($\pm$ 0.01)	0.12 ($\pm$ 0.02)	0.17 ($\pm$ 0.03)	0.13 ($\pm$ 0.03)	0.07 ($\pm$ 0.02)
2006-2010	0.35 ($\pm$ 0.05)	0.14 ($\pm$ 0.03)	0.01 ($\pm$ 0.01)	0.09 ($\pm$ 0.02)	0.03 ($\pm$ 0.01)	0.05 ($\pm$ 0.01)	0.13 ($\pm$ 0.02)	0.15 ($\pm$ 0.03)	0.10 ($\pm$ 0.02)	0.07 ($\pm$ 0.02)
2007-2011	0.39 ($\pm$ 0.05)	0.20 ($\pm$ 0.04)	0.01 ($\pm$ 0.01)	0.17 ($\pm$ 0.02)	0.04 ($\pm$ 0.02)	0.03 ($\pm$ 0.01)	0.15 ($\pm$ 0.02)	0.10 ($\pm$ 0.02)	0.15 ($\pm$ 0.03)	0.06 ($\pm$ 0.02)
2008-2012	0.40 ($\pm$ 0.05)	0.17 ($\pm$ 0.03)	0.03 ($\pm$ 0.01)	0.12 ($\pm$ 0.02)	0.05 ($\pm$ 0.02)	0.00 ($\pm$ 0.01)	0.12 ($\pm$ 0.02)	0.11 ($\pm$ 0.02)	0.15 ($\pm$ 0.02)	0.07 ($\pm$ 0.01)
2009-2013	0.38 ($\pm$ 0.05)	0.24 ($\pm$ 0.04)	0.02 ($\pm$ 0.01)	0.08 ($\pm$ 0.01)	0.09 ($\pm$ 0.02)	0.00 ($\pm$ 0.00)	0.09 ($\pm$ 0.02)	0.13 ($\pm$ 0.02)	0.16 ($\pm$ 0.03)	0.08 ($\pm$ 0.02)
2010-2014	0.40 ($\pm$ 0.06)	0.26 ($\pm$ 0.05)	0.08 ($\pm$ 0.02)	0.14 ($\pm$ 0.02)	0.09 ($\pm$ 0.02)	0.01 ($\pm$ 0.00)	0.08 ($\pm$ 0.02)	0.10 ($\pm$ 0.02)	0.19 ($\pm$ 0.03)	0.04 ($\pm$ 0.01)
2011-2015	0.42 ($\pm$ 0.06)	0.31 ($\pm$ 0.05)	0.03 ($\pm$ 0.01)	0.11 ($\pm$ 0.01)	0.03 ($\pm$ 0.01)	0.01 ($\pm$ 0.01)	0.11 ($\pm$ 0.03)	0.07 ($\pm$ 0.02)	0.32 ($\pm$ 0.04)	0.07 ($\pm$ 0.02)
2012-2016	0.40 ($\pm$ 0.05)	0.38 ($\pm$ 0.04)	0.01 ($\pm$ 0.01)	0.07 ($\pm$ 0.01)	0.04 ($\pm$ 0.01)	0.01 ($\pm$ 0.01)	0.11 ($\pm$ 0.03)	0.14 ($\pm$ 0.03)	0.23 ($\pm$ 0.03)	0.03 ($\pm$ 0.01)
2013-2017	0.40 ($\pm$ 0.05)	0.31 ($\pm$ 0.04)	0.00 ($\pm$ 0.00)	0.06 ($\pm$ 0.01)	0.24 ($\pm$ 0.03)	0.01 ($\pm$ 0.00)	0.08 ($\pm$ 0.02)	0.15 ($\pm$ 0.03)	0.10 ($\pm$ 0.03)	0.04 ($\pm$ 0.01)
1997-2017	0.43 ($\pm$ 0.03)	0.23 ($\pm$ 0.03)	-	0.04 ($\pm$ 0.01)	0.08 ($\pm$ 0.02)	0.03 ($\pm$ 0.01)	0.06 ($\pm$ 0.01)	0.18 ($\pm$ 0.02)	0.08 ($\pm$ 0.02)	0.12 ($\pm$ 0.02)

Table S4 Summary of the results of the generalized least squares models with Auto Regressive Moving Average (ARMA), showing the time dependence of the contribution of each landscape metric. Significant trends are represented by solid lines in Figs 4 & S2.

Landscape metric	Type of autocorrelation	Independent variable	F value	numDf	p value	Coef $\pm$ SE
Cereal density	ARMA(q=1)	(Intercept)				(0.299 $\pm$ 0.018)
		Time	60.533	1	<0.001	-0.037 $\pm$ 0.005
		Time ²	96.173	1	<0.001	0.002 $\pm$ 0.000
Rape density	ARMA(q=1)	(Intercept)				(0.035 $\pm$ 0.014)
		Time	0.243	1	0.629	
		Time ²	0.942	1	0.348	
Meadow density	ARMA(q=1)	(Intercept)				(0.090 $\pm$ 0.017)
		Time	0.080	1	0.782	
		Time ²	0.051	1	0.825	
Crop diversity	ARMA(q=1)	(Intercept)				(0.011 $\pm$ 0.015)
		Time	9.194	1	0.008	0.004 $\pm$ 0.001
		Time ²	3.449	1	0.085	
Patch size	ARMA(q=2)	(Intercept)				(0.171 $\pm$ 0.028)
		Time	16.993	1	<0.001	-0.011 $\pm$ 0.003
		Time ²	0.068	1	0.799	
Hedgerow density	ARMA(q=1)	(Intercept)				(-0.011 $\pm$ 0.023)
		Time	9.611	1	0.008	0.023 $\pm$ 0.006
		Time ²	10.070	1	0.007	-0.001 $\pm$ 0.000
Distance to woodland	ARMA(q=1)	(Intercept)				(0.184 $\pm$ 0.020)
		Time	5.219	1	0.037	-0.004 $\pm$ 0.002
		Time ²	0.488	1	0.496	
Road density	ARMA(q=1)	(Intercept)				(0.011 $\pm$ 0.035)
		Time	11.605	1	0.004	0.012 $\pm$ 0.003
		Time ²	0.535	1	0.477	
Distance to buildings	ARMA(q=2)	(Intercept)				(0.203 $\pm$ 0.035)
		Time	9.786	1	0.007	-0.010 $\pm$ 0.003
		Time ²	0.244	1	0.629	

Table S5 Raw numbers (and associated %) of partridge sightings according to the range of values of each landscape metric, for each of four contiguous windows (1997-2001, 2002-2006, 2007-2011 and 2012-2016).

Landscape metric	Range of value	1997 – 2001	2002 – 2006	2007 – 2011	2012 – 2016
Cereal density	< 0.25	30 (13%)	22 (12%)	18 (8%)	9 (7%)
	0.25 – 0.75	200 (87%)	162 (88%)	188 (89%)	110 (90%)
	> 0.75	1 (0%)	0 (0%)	6 (3%)	2 (2%)
Distance to woodland (m)	< 250	34 (15%)	30 (16%)	36 (17%)	27 (22%)
	250 – 1000	168 (73%)	139 (76%)	163 (77%)	91 (75%)
	> 1000	29 (12%)	15 (8%)	13 (6%)	3 (2%)
Road densities (m/ha)	< 20	42 (18%)	31 (17%)	36 (17%)	13 (11%)
	20 – 200	187 (81%)	153 (83%)	176 (83%)	108 (89%)
	> 200	2 (1%)	0 (0%)	0 (0%)	0 (0%)
Distance to buildings (m)	< 160	29 (13%)	37 (20%)	34 (16%)	26 (21%)
	> 160	202 (87%)	147 (80%)	178 (84%)	95 (79%)

Table S6 Ranges and means of landscape metrics above the cutoff used to identify values of landscape metrics selected by grey partridge (see Methods for details) in four contiguous five-year periods.

Period	1997 – 2001	2002 – 2006	2007 – 2011	2012 – 2016
Cutoff	0.564	0.515	0.483	0.496
Range of selected cereal densities	0.24-0.85	0.18-0.75	0.23-1.00	0.30-0.77
Mean selected cereal density	0.55	0.47	0.62	0.54
Range of selected distances to woodland (m)	340-1285	175-1350	170-1700	250-1060
Mean selected distance to woodland (m)	820	765	935	660
Range of selected road densities (m/ha)	<270	<200	20-170	35-165
Mean selected road density (m/ha)	137	99	96	99
Range of selected distances to nearest building (m)	>160	>0	>0	>0
Mean selected distance to nearest building (m)	1010	910	910	910

Table S7 Mean size (min; max) and mean habitat suitability Index of suitable patches for grey partridge over time. The similarity between habitat suitability maps of 1997 – 2001 (taken as reference) and each subsequent five-year window was assessed as Schoener's D. The threshold used to discriminate suitable from unsuitable patches is the cutoff of models calibrated for 1997-2001, i.e. 0.564 (see section Material and Methods).

Time period	Mean size (min; max) of suitable patches	Mean habitat suitability index of suitable patches	Schoener's D
1997-2001	26.40 ha (4; 1280)	0.696	–
1998-2002	26.15 ha (4; 1416)	0.697	0.945
1999-2003	25.98 ha (4; 1080)	0.693	0.928
2000-2004	25.01 ha (4; 1120)	0.695	0.906
2001-2005	23.73 ha (4; 1112)	0.697	0.893
2002-2006	24.18 ha (4; 1212)	0.697	0.872
2003-2007	24.12 ha (4; 1328)	0.697	0.865
2004-2008	24.83 ha (4; 1848)	0.694	0.853
2005-2009	23.76 ha (4; 1560)	0.692	0.848
2006-2010	23.54 ha (4; 1408)	0.692	0.840
2007-2011	22.04 ha (4; 968)	0.689	0.835
2008-2012	21.05 ha (4; 916)	0.688	0.825
2009-2013	21.66 ha (4; 936)	0.687	0.821
2010-2014	21.05 ha (4; 1088)	0.689	0.816
2011-2015	20.51 ha (4; 1152)	0.685	0.814
2012-2016	20.63 ha (4; 1180)	0.687	0.813
2013-2017	19.60 ha (4; 992)	0.682	0.815

Appendix B. Selection of uncorrelated explanatory variables.

Explanatory variables, especially when numerous, are potentially highly intercorrelated (Barbet-Massin & Jetz, 2014). We used the method published by Leroy et al. (2013) to select uncorrelated variables (see Table S1 for details of the variables used): (1) identify groups of intercorrelated variables using a hierarchical ascendant classification on a distance metric calculated from the Pearson's correlation coefficient; (2) within each group of intercorrelated variables, select the variable having the highest contribution to the prediction of occurrence.

As this selection procedure was performed on a dataset with pixels with sightings (presence) plus the pixels selected as pseudo-absences (Leroy et al., 2013), the results can be sensitive to the number of pseudo-absences generated. Barbet-Massin et al. (2012) recommend generating either 1 dataset with 10000 pseudo-absences or at least 10 datasets with 1000 pseudo-absences. The correlated groups were identified using both numbers of pseudo-absences.

1. Identification of groups of intercorrelated landscape metrics

From the presence and pseudo-absence pixels, we calculated the Pearson's correlation coefficient (r) between each pair of variables. We then performed a hierarchical ascendant classification using a distance metric ($1-r$) to identify groups of intercorrelated variables. Leroy et al. (2013) used a correlation threshold of 0.7 (distance < 0.3) above which variables are considered as intercorrelated. In our analysis we will consider a more restrictive correlation threshold of 0.5 (distance < 0.5) as recommended by Barbet-Massin & Jetz (2014) to minimize correlation between predictors. This procedure was carried out for the whole 21-year period (1997-2017), and also for the 17 five-year windows (from 1997-2001 to 2013-2017), to ensure that variables were not intercorrelated over the study period. For either number of pseudo-absences, all variables were considered as uncorrelated for the 5-year moving windows, but cereal density and rape density were correlated for the whole 21-year period.

2. Selection of variables within the groups of intercorrelated variables

This second step was only carried out for the whole 21-year period as the variables were not correlated in the 5-year windows. To identify the highest contributive variable within each group of intercorrelated variables, models were calibrated with only the intercorrelated variables and their contributions were assessed using the *biomod2 variables_importance*

function (Leroy et al., 2013). For a given variable, a standard prediction is made with a model calibrated with the intercorrelated variables, and then a series of predictions are made with randomized values of the given variable. The contribution of the variable to each prediction is 1 less the correlation with the standard prediction; the higher the correlation, the weaker the contribution or predictive power of the variable. Ten replications of the randomization procedure were used (Leroy et al., 2013). Finally, the variable with the highest contribution was selected.

Cereal density (contribution of 0.56 for 1000 pseudo-absences and 0.55 for 10000 pseudo-absences generated) was kept while rape density (contribution of 0.37 for 1000 pseudo-absences and 0.47 for 10000 pseudo-absences generated) was discarded. This choice is also consistent with the known biology of partridges which prefer cereal cover during the breeding period.

Appendix C. Selection of the method for pseudo-absence generation, the number of pseudo-absences, and the modeling technique

Modeling techniques of habitat suitability require presence and absence data. As our dataset did not contain true absences, pseudo-absences were generated. One recommendation is to generate either 10000 pseudo-absences in one dataset or at least 1000 pseudo-absences in 10 datasets by random sampling (Barbet-Massin et al., 2012). This method has been criticized for introducing bias (Phillips et al., 2009) so we also used the “disk” method in *biomod2* to generate pseudo-absences in areas which had been prospected and where no presence were recorded: within a radius of 1 km around pixels with presences (Phillips et al., 2009; Zaniwski, Lehmann, & Overton, 2002).

Then, to produce response curves, we had to select a modeling technique. The modeling technique must be selected according to the predictive performance, the ease of use, the comprehensibility, and the ease of interpretation of the outputs (Elith et al., 2005). In this step, seven modeling techniques commonly used in *biomod2* were tested: three used regressions, generalized linear model (GLM), generalized additive model (GAM), multiple adaptive regression splines (MARS); two used classifications: classification tree analysis (CTA), flexible discriminant analysis (FDA); and two used machine-learning: random forest (RF) and generalized boosting model (GBM) (Barbet-Massin et al., 2012; Leroy et al., 2013; Monnet et al., 2015). Models were calibrated with default options for all the uncorrelated explanatory variables. The true skill statistic (TSS) (Allouche et al., 2006) is commonly used for species distribution model evaluation. $TSS = specificity + sensitivity - 1$, where the specificity is the proportion of absences well predicted by the model, and the sensitivity is the proportion of presences well predicted by the model (Allouche et al., 2006). The TSS / sensitivity pair can be used to select a model (Barbet-Massin et al., 2012). A modeling technique with a high TSS and a high sensitivity will be preferred to a modeling technique with a high TSS and a high specificity. The TSS and the sensitivity were assessed for each of the modeling techniques, for all combinations of the pseudo-absence generation method (“random”, “disk”) and the number of pseudo-absences generated per dataset (1000, 10000) (Table S8).

Firstly, for any period, either number of pseudo-absences, and any type of modeling technique, the TSS and sensitivity were higher when pseudo-absences were generated by random sampling (Table S8). This is consistent with the recommendation to prefer random

sampling when true absences are unavailable (Barbet-Massin et al., 2012). Therefore, random sampling was selected.

Secondly, for any period, when pseudo-absences were randomly generated, the number of pseudo-absences per dataset had little effect on the TSS and sensitivity of the models, but 10 datasets of 1000 pseudo-absences seemed to give slightly better and more stable results over the study periods (Table S8). As generating of 1000 pseudo-absences in each dataset provides replication, and is faster, we used datasets with 1000 random pseudo-absences as is usual (Leroy et al., 2013; Monnet et al., 2015).

Thirdly, we selected a model using two criteria. The first was its suitability for drawing response curves: this requires a good predictive performance (Elith et al., 2005) and stability over the study period. Overall, all the modeling techniques had a similar predictive performance (Table S8). The regression techniques were more stable for both TSS and sensitivity and less influenced by the number of pseudo-absences per dataset. These results are consistent with Barbet-Massin et al. (2012) who found that GLMs and GAMs are not influenced as much as other modeling techniques by the number of pseudo-absences. These methods yielded the best sensitivity too.

The second criterion is that the technique should be easy to use and understand (Elith et al., 2005). As the shape of the response curves and the variation in model coefficients with time were the main outputs on interest, GLMs and GAMs are to be preferred as the predicted response to each variable does not depend on the other variables, unlike modeling technique with no inherent structure, or regression trees and MARS with interaction terms that may not be fitted to the entire range of each variable but on several segments of the variable (Elith et al. 2005). For these reasons, we selected GLM which was stable, performed as well as the others, had one of the best sensitivities, is easy to use and understand, is easy to parameterize, provides easy interpretable response curves (Elith et al. 2005) and is compatible with datasets with 1000 randomly generated pseudo-absences (Barbet-Massin et al., 2012). In order to obtain reliable confidence intervals, 100 datasets were used in the final modeling process.

Table S8 Performance of the various modeling techniques (GLM, GAM, MARS, CTA, FDA, RF, GBM) and average performance over these techniques taken together (“mean”) measured as the TSS (true skill statistic) and the sensitivity as a function of the method used to generate pseudo-absences, the number of pseudo-absences, and the period.

		Random										Disk									
		1997-2001		2002-2006		2007-2011		2012-2016		1997-2017		1997-2001		2002-2006		2007-2011		2012-2016		1997-2017	
		TSS	Sens.	TSS	Sens.	TSS	Sens.	TSS	Sens.	TSS	Sens.	TSS	Sens.	TSS	Sens.	TSS	Sens.	TSS	Sens.	TSS	Sens.
10*1,000 PA	GLM	0.43	70.36	0.44	76.92	0.40	74.29	0.42	77.20	0.43	74.98	0.38	66.91	0.37	66.72	0.33	72.99	0.35	77.73	0.38	71.02
	GAM	0.44	73.61	0.43	75.77	0.36	74.81	0.40	78.94	0.44	75.62	0.36	64.02	0.35	70.95	0.31	68.92	0.35	75.00	0.38	72.59
	MARS	0.45	71.97	0.42	75.77	0.37	72.34	0.35	77.88	0.44	76.24	0.38	68.92	0.33	67.71	0.26	62.42	0.29	70.98	0.38	73.29
	CTA	0.35	69.72	0.38	66.42	0.33	67.75	0.33	64.24	0.41	73.81	0.30	63.61	0.31	62.44	0.27	64.59	0.28	61.59	0.36	71.96
	FDA	0.44	70.98	0.40	75.72	0.39	71.30	0.37	74.85	0.43	76.46	0.37	66.63	0.33	65.92	0.32	69.00	0.29	68.86	0.39	70.90
	RF	0.49	73.25	0.46	69.95	0.42	70.04	0.42	65.45	0.52	72.69	0.42	65.66	0.39	60.55	0.35	56.93	0.38	60.23	0.49	68.12
	GBM	0.48	66.10	0.49	77.01	0.43	76.62	0.46	74.62	0.47	77.68	0.42	70.32	0.39	67.96	0.36	67.97	0.40	70.61	0.42	74.36
	mean	0.44	70.98	0.43	73.94	0.39	72.45	0.39	73.31	0.45	75.35	0.38	66.58	0.35	66.03	0.31	66.12	0.34	69.29	0.40	71.75
1*10,000 PA	GLM	0.44	71.89	0.44	73.13	0.36	65.80	0.37	76.52	0.42	77.48	0.39	70.28	0.38	67.16	0.35	65.80	0.31	81.82	0.39	75.45
	GAM	0.45	77.91	0.43	77.11	0.36	75.76	0.39	75.00	0.45	79.50	0.37	69.48	0.30	76.12	0.27	59.31	0.33	78.03	0.38	73.87
	MARS	0.45	79.91	0.41	78.61	0.34	59.74	0.40	73.49	0.44	76.35	0.37	65.46	0.32	69.65	0.33	63.20	0.34	77.27	0.39	70.95
	CTA	0.32	59.04	0.41	68.66	0.36	65.80	0.34	61.36	0.42	63.96	0.29	50.60	0.36	60.70	0.30	75.32	0.25	59.85	0.41	69.48
	FDA	0.40	71.08	0.38	73.63	0.38	67.10	0.30	69.70	0.42	73.42	0.38	71.89	0.34	70.65	0.29	59.31	0.30	69.70	0.37	66.67
	RF	0.40	73.09	0.43	60.20	0.35	65.37	0.25	56.82	0.50	61.49	0.39	68.27	0.33	45.77	0.32	51.95	0.41	59.09	0.49	64.08
	GBM	0.49	75.10	0.47	76.12	0.41	69.70	0.45	75.00	0.48	81.08	0.43	70.28	0.38	81.59	0.36	56.71	0.39	65.91	0.43	75.90
	mean	0.42	70.97	0.42	72.49	0.36	67.04	0.36	69.70	0.45	73.33	0.37	66.61	0.34	67.38	0.32	61.66	0.33	70.24	0.41	70.91

Chapitre II
Compétition interspécifique entre la Perdrix
grise et la Perdrix rouge dans un paysage
agricole

Avant-propos et résumé du Chapitre II

La compétition interspécifique, déterminant majeur des interactions trophiques, des niches écologiques, et des processus évolutifs, est particulièrement attendue entre espèces phylogénétiquement proches partageant une ou plusieurs ressources. Chez les oiseaux, cette compétition prend souvent la forme d'une compétition médiée par le chant, et induit souvent des conséquences asymétriques pour les espèces impliquées. Dans les milieux agricoles, l'intensification des pratiques a considérablement affecté la qualité de l'habitat (couverts d'alimentation, couverts refuges, sites de nidification), limitant la capacité d'accueil pour les oiseaux (voir Chapitre I). Bien qu'une augmentation de la pression de compétition dans les patches d'habitats favorables restants soit attendue, très peu d'études s'y sont intéressées.

Dans ce Chapitre II, nous avons examiné si une compétition interspécifique existe entre les Perdrix grise et rouge, deux espèces phylogénétiquement et écologiquement proches, originellement parapatriques, mais dont la zone de contact a été artificiellement augmentée par des lâchers cynégétiques fréquents en Europe de l'Ouest. Les comportements territoriaux des deux espèces ont été étudiés par points d'écoute avec repasse audio, analysés, et les conséquences en termes de déplacement de niche ont été évaluées.

Nos résultats suggèrent une compétition asymétrique entre les deux espèces. En situation de co-occurrence, la Perdrix grise est moins territoriale (taux de réponse et intensité du comportement territoriale plus faibles), alors que la Perdrix rouge maintient son comportement territorial. Des conséquences asymétriques ont également été relevées. La niche de la Perdrix grise est déplacée dans la direction opposée au cœur de niche de la Perdrix rouge, alors que cette dernière ne modifie pas sa niche en situation de co-occurrence avec la Perdrix grise.

Ces résultats soulignent l'importance de repenser la gestion cynégétique vers une amélioration de l'habitat afin d'en augmenter la capacité d'accueil et de diluer la pression de compétition. Nous suggérons également d'engager une réflexion visant à limiter les lâchers simultanés d'espèces phylogénétiquement proches, afin de limiter la compétition qui pourrait interférer avec le recouvrement de populations viables. Plus globalement, cette étude souligne la nécessité de prendre en considération la présence de compétiteurs comme potentielle limite au recouvrement des populations en gestion et en conservation.

**Interspecific competition between grey (*Perdix perdix*) and
red-legged (*Alectorix rufa*) partridges in agricultural landscape**

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Abstract

Interspecific competition is expected to occur between phylogenetically close species sharing resources. In birds, interspecific competition often occurs by interference mediated by song, and frequently implies asymmetrical outcomes for species involved. Despite the loss of habitat quality resulting from agricultural intensification could have concentrated bird species in the remaining suitable habitats, the hypothesis of interspecific competition has rarely been considered as potential additional factor limiting bird population recovery in farmland landscapes.

Grey and red-legged partridges, phylogenetically related species, were originally parapatric but an artificial increase in their contact zone has occurred in Western Europe due to huge human-mediated gamebird releases. Despite grey partridge has suffered a large-scale decline in Europe since the 1950s attributed to the decrease in holding capacity of habitats triggered by agricultural intensification, the hypothesis of interspecific competition on the few remaining suitable habitats remains unexplored. This study investigated whether and how an interspecific competition could occur between both partridge species. We recorded territorial behaviours through a playback stimuli experiment, analyzed territorial behaviour, and

investigated outcomes on ecological niche in absence *versus* co-occurrence with the hypothetic competitor.

Our results showed behavioural clues in favor of an asymmetric competition benefiting to red-legged partridge. Grey partridge became less territorial in co-occurrence with red-legged partridge while no change in the territorial behaviour of red-legged partridge was detected. In co-occurrence areas, both species changed their pattern of daily territorial activity toward narrower period of territorial responses. Asymmetric outcomes were also reported, with a shift in the grey partridge's niche in the opposite direction of the core of the red-legged partridge's niche in co-occurrence areas possibly impairing its access to habitats, while the red-legged partridge's niche remained consistent.

This study highlights the need to rethink game management towards habitat improvement aiming at increasing the habitat holding capacity and dilute competition pressure, and towards a limitation of simultaneous release of multiple species to prevent interspecific competition which could interfere with, and imperil the recovery of sustainable populations. It further emphasizes the need to account for the presence of potential competitors as a limit to the population recovery in translocation and conservation programs.

Key words

Asymmetric competition, Grey partridge, Niche displacement, Playback experiment, Red-legged partridge, Territorial behaviour.

Introduction

Interspecific competition is a major driver of trophic interactions, ecological niches, biogeographic patterns and evolutionary processes (Bull, 1991; Dhondt, 2012; Jankowski, Robinson, & Levey, 2010; MacArthur & Levins, 1964; Martin, Freshwater, & Ghalambor, 2017; Martin & Martin, 2001b; Wiens, 1992). Interspecific competition is expected to occur between phylogenetically close species, either directly through agonistic interactions (Martin et al., 2017; Persson, 1985; Wiens, 1992) or indirectly through resource depletion (Dhondt, 2012; Schoener, 1983; Wiens, 1992). Recent decline in habitat quality in rural landscapes, resulting from post-war changes in agricultural practices, has not only triggered decline of European farmland birds (Benton, Vickery, & Wilson, 2003; Newton, 2004; Robinson & Sutherland, 2002), but has also concentrated birds to local remaining suitable habitat patches (Aebischer & Ewald, 2012), increasing the likelihood of interspecific competition to occur. Though, this possibility remained surprisingly largely unexplored in agricultural landscape (but see Robillard, Garant, & Bélisle, 2013).

Outcomes of interspecific relationships in vertebrates are in most cases asymmetric, favoring a species more than the other (Martin et al., 2017; Pasch, Bolker, & Phelps, 2013; Persson, 1985; Schoener, 1983). For instance, 224 out of 270 pairs of phylogenetically close bird species showed asymmetric outcomes from interspecific interactions, benefitting the larger species in 87% of the cases (Martin et al., 2017). Typically, larger and dominant species show little difference in the territorial response (vocal behavior and approaches) to the heterospecific *versus* conspecific song, while the smaller subordinate species show lower responses to the heterospecific *versus* conspecific song (Martin & Martin, 2001a; McEntee, 2014). This may result in a shift in the song schedule to avoid territorial interaction (Brumm, 2006; Cody & Brown, 1969), and in the displacement and/or contraction of the ecological niche of the subordinate species (Jankowski et al., 2010; Martin & Martin, 2001b; Svärdsön, 1949; Tarjuelo, Traba, Morales, & Morris, 2017). Such asymmetric interspecific relationships outcome may impact population dynamics of subordinate species, by constraining its distribution to lesser quality habitats yielding lower breeding success (Martin & Martin, 2001a, 2001b).

Grey partridge *Perdix perdix* L. 1758 and red-legged partridge *Alectoris rufa* L. 1758 are phylogenetically related and belong to the *Phasianidae* (Wang et al., 2013). They were

originally parapatric, showing separated but contiguous distributions (Cramp & Simmons, 1980; see also Bull, 1991; Watson, 1962), with grey originating from central Europe and Asia (Liukkonen-Anttila, Uimaniemi, Orell, & Lumme, 2002) and red-legged from Iberia (Ferrero et al., 2011). The contact zone between their distributions was restricted to central and southern France and north-west Italy (Cramp & Simmons, 1980). However, huge releases of red-legged partridge as gamebirds in the UK and France (Cramp & Simmons, 1980) brought both species being currently sympatric over vast areas. They select open agricultural landscapes (Aebischer & Kavanagh, 1997; Aebischer & Lucio, 1997; Potts, 1980), have similar breeding habitats (Bro et al., 2013; Green, Rands, & Moreby, 1987; Meriggi et al., 1991; Rands, 1988), despite slight differences in micro-habitat exist (Meriggi et al., 1991), and overlap in their breeding phenology (egg laying in May-June, peak of territorial activity in February-April; Rotella & Ratti, 1988). In addition, chicks feed on the same arthropod taxa, and adults shift to leaves and seeds (Bro & Ponce-Boutin, 2004; Green, 1984; Green et al., 1987). Finally, partridges are highly territorial, with both mates contributing to territory defense (Casas, Arroyo, Viñuela, Guzmán, & Mougeot, 2016; Potts, 1980). The original narrow contact zone between both species was suggestive of the presence of competition interactions (Bull, 1991; Watson, 1962), now expected to be more present over the entire and vast contact zone (Jankowski et al., 2010; Martin & Martin, 2001a; McEntee, 2014).

The possible increasing competition pressure in grey partridge with the larger and bulkier red-legged partridge in the human-created contact zone by the introduction of the latter non-native (Carpio et al., 2017; Robertson, 1996; Sokos, Birtsas, & Tsachalidis, 2008), has rarely been studied as a possible cause of grey partridge decline or limitation for population recovery (Bro, 2016; Meriggi et al., 1991). Indeed, grey partridge is one the most iconic farmland bird in Europe (Sotherton, Aebischer, & Ewald, 2014), but has strongly declined (Aebischer & Kavanagh, 1997; Aebischer & Potts, 1994) and is now threatened (Eaton et al., 2015; Hagemeyer & Blair, 1997). In this study, we aimed at investigating interspecific competition between the two partridges in study areas located in the natural range of co-occurrence (central western France). We quantified territorial behaviour through playback stimuli, analyzing the patterns of territorial response in mono- and inter-specific situations (Cody & Brown, 1969; Martin & Martin, 2001a), and further investigated niche shifts in cases of co-occurrence. If asymmetric interspecific competition occurs with domination by the larger

species, we predicted that grey partridge should respond less to red-legged partridge than to the conspecific song in absence or co-occurrence of red-legged partridge, and should adopt a more discreet territorial behaviour in co-occurrence areas. Conversely, red-legged partridge should increase its response to grey partridge in co-occurrence situations, and maintain or increase its territorial behaviour. We also predicted that grey partridge should restrict their daily activity pattern when closely associated with red-legged partridge to minimize inter-specific encounters. Finally, habitat segregation and ecological niche of the subordinate grey partridge should shift when in co-occurrence with red-legged partridges, while the dominant red-legged partridge should be unaffected by the presence of grey partridge.

Material & methods

Study area

The study was conducted on the Long-Term Socio-Ecological Research (LTSER) Zone Atelier « Plaine & Val de Sèvre » (hereafter, ZAPVS), central western France, (Fig. 1; Bretagnolle et al., 2018b), in 2016 and 2017. This area is an intensive cereal plain of 435 km² (excluding the Chizé forest), cropped by winter cereals (41.5%), sunflower (10.4%), maize (9.6%), rape (8.3%), meadows (13.5%), woodlands (2.9%) and built-up areas (9.8%; average values 2009-2016 Bretagnolle et al., 2018b). Within the ZAPVS, a restricted study site of 34km² (2016) to 68 km² (2017) was chosen where both partridges species were historically most observed during the past two decades (Fig. 1). In 2017, a second study site, with higher density of partridges than in the ZAPVS, was added to increase the dataset of sightings (Table S1, Appendix A); this second site is close to the ZAPVS to keep homogeneity in birds' phenology, and with similar habitat types. This site of 18 km² is located in the south of Maine-et-Loire (METL; Fig. 1).

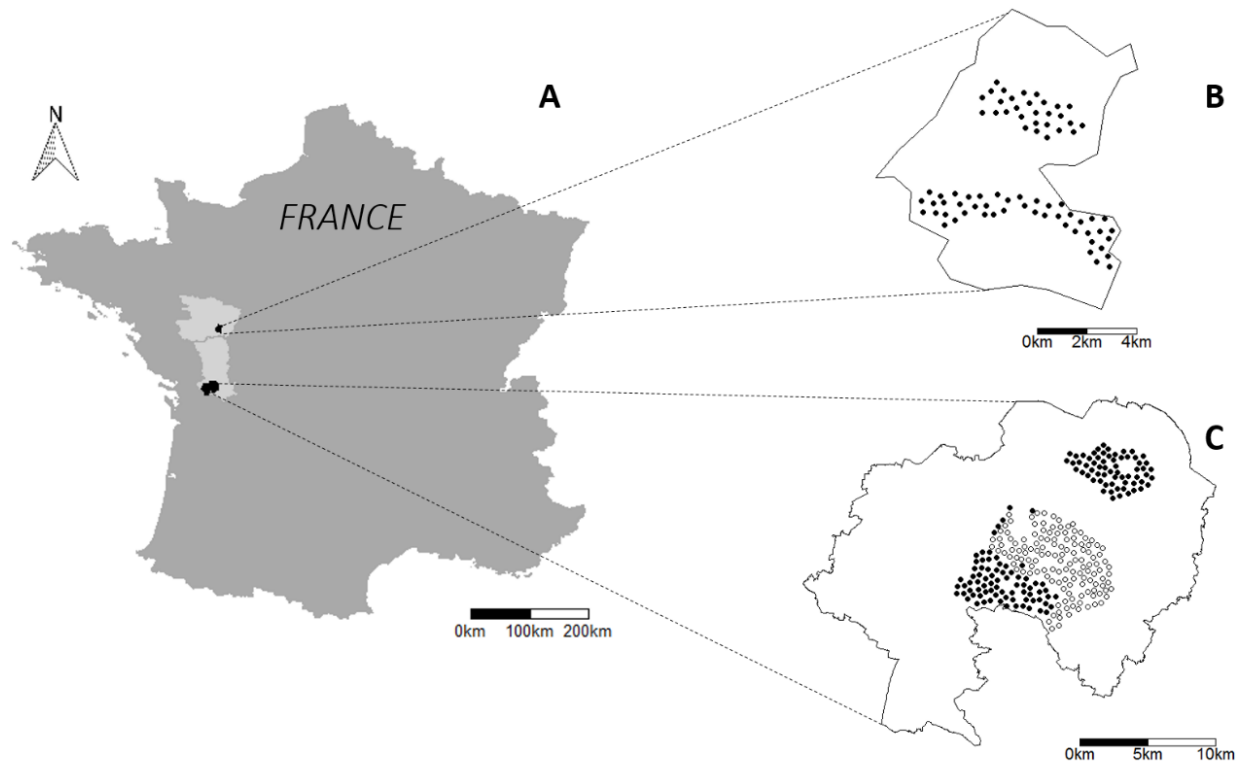


Figure 1 (a) Location of the two study sites in the Maine-et-Loire (1b) and Deux-Sèvres (1c) departments, central western France. (b) Distribution of the point count stations in Maine-et-Loire. (c) Distribution of the point count stations on the LTSER Zone Atelier "Plaine & Val de Sèvre". White dots refer to points sampled from 2016 to 2017, black dots refer to points sampled in 2017 only.

Survey protocol and playback tests

We first established a grid of playback stations with a pixel size of 500 m (excluding built-up areas) to locate accurately territorial pairs. Sample points were placed as close as possible to the centroid of the grid cells, but still on a path or a road for access ease and disturbance minimization. Each sample point was replicated four times per season, with two sessions in the morning and two in the evening, as patterns of daily vocal activity peak at dawn and dusk (Pépin & Fouquet, 1992). Sample points were slowly approached by car, the observer went out without noise and waited for 1 minute before starting a session. A session consisted in the broadcasting, at fixed volume (calibrated to be heard up to 250 meters to avoid overlap between neighboring points) with a NEWONLINE N74® speaker, of an audio sequence containing territorial calls of males of both study species (155 seconds for each species), and the Common quail *Coturnix coturnix* L. 1758 call as control. Each species bouts were separated by 1-min silence (see Appendix B for more details about sequence preparation and song origins). Given three species were broadcasted, six audio sequences containing the six possible broadcasting layouts, were prepared and randomly played at each session. In 2016, 140

playback stations were surveyed on ZAPVS (April 6 to April 25), while in 2017, 275 stations were surveyed inside the ZAPVS and 75 in the METL, from March 14 to April 28. Points were arranged in tracks of 14-17 survey points along a road/path, with a track corresponding to a sequence of points made in a morning or evening session. Routes along tracks were made alternately in a way then in the other, to avoid hourly biases.

Then, for each point a given year, we determined whether none, one or the two species were present at least once over the four sampling sessions. Points were then classified into four disjoint categories as to whether only one, none or both partridges were contacted. This latter category was discarded, so that only points with at least one occurrence were kept for analyses, assuming that a species was absent of a point if no sightings were recorded in this point over the four sampling sessions. We checked whether discarded points may actually contain partridges using rarefaction curve analyses (see Appendix C): only 7.3% and 12.5% of points for grey and red-legged partridges, respectively, may have actually been withdrawn erroneously. For each individual contacted on a point, we reported the playback call that elicited the response, the type of response (0: no response, 1: response to one of the partridge species calls, 2: response to both partridge stimuli), the latency of response (elapsed time between the beginning of the playback and the territorial response) and the territorial behaviour (walking approach, flight approach, calling).

Partridge niche analysis

The ecological niche analysis was based on three datasets of occurrences of grey and red-legged partridges collected by fieldworkers on the ZAPVS between 2013 and 2017. A first dataset contains occurrences from systematic bird point counts without playback (see Brodier, Augiron, Cornulier, & Bretagnolle, 2014 for protocols). About 450 points spread all over the ZAPVS were sampled each year during the passerine breeding period (Bretagnolle et al., 2018a). The second dataset contains opportunistic sightings when fieldworkers studying other bird species saw partridges (Bretagnolle et al., 2018b), or during the land cover monitoring performed twice a year systematically over the entire study site (see Harmange, Bretagnolle, Sarasa, & Pays, 2019). Each year, opportunistic monitoring occurred daily from late March to late July. The third dataset contains partridge sightings from the playback

experiment (see above). Cumulating the three data sets, a total of 262 and 457 presence locations were available for grey and red-legged partridges, respectively.

From the land cover data collected annually, we then created a grid of 600*600 m² cells, using R (R Core Team, 2017) and QGIS (Quantum GIS Development Team, 2017), excluding all pixels that included less than half in surface (18 ha) intersecting with the study site. Pixel size was chosen as the minimal pixel size that enable to obtain sufficient numbers of pixels containing only grey partridge over the period 2013-2017 (n = 115), containing only red-legged partridge occurrences (n = 137), or containing occurrences of both partridge species (n = 32). Landscape metrics analyzed were chosen among those identified being selected (either positively or negatively) in grey and/or red-legged partridges (Birkan, Serre, Skibnienski, & Pelard, 1992; Bro et al., 2013; Harmange et al., 2019; Meriggi et al., 1991; Rands, 1987): cereals, rape, meadows, spring crops (corn, sunflower etc.), hedgerows, roads/tracks, woodlands and buildings. Landscape metrics used in analyses corresponded to surface (or total length in m) of each habitat contained in the pixel divided by the pixel surface in case of surfaces (to account for edge effect). Each parameter was calculated annually from 2013 to 2017, except for roads and hedgerows which remained stable and for which we set only one layer (Harmange et al., 2019).

Statistical analyses

Presence/absence of territorial response (vocalization and/or approach) was modeled with GLMMs (binomial response variable, logit link) as a function of the interaction between species playback and species composition of the point, depending on broadcasted species (target species *alone* or *co-occurrence* with the other species). The playback *sequence* (6 modalities) and the *rank* of partridge song (1st position, 2nd position) were considered as a random factors. For each species, we further analyzed the magnitude of territorial response, described by four parameters. These included *territorial response rate* (number of responding individuals within the pair), *response latency*, *calling behaviour* (0: no response, 1: response to one of the two partridge species calls, 2: response to both partridge stimuli) and a *territoriality score* in the form of a ranking of increasing territorial behavior intensity (0: no response, 1: approach, 2: vocalization, 3: approach with vocalization, 4: flying approach with vocalization; see Table S2 in Appendix A for more details about variable calculations). Then,

for each species, we carried out linear discriminant analyses (LDA) with cross-validation (e.g. Germain & Laurin, 2005) to investigate whether territorial behaviour (from the four previous behavioural variables) allowed to discriminate between situations where a single species was present compared to situations of co-occurrence. Then, to complete this descriptive analysis, we carried out analyses of variance (ANOVA) on each behavioural variable to investigate and test which territorial behaviour among the four behavioural variables best discriminated both situations (species alone or in co-occurrence).

To investigate the daily pattern of territorial behaviour for each species, we first summed the number of territorial responses (vocal behaviour and approaches) on a half-hour time lag, according to four modalities: grey partridge alone and grey co-occurring with red-legged partridge, and red-legged partridge alone and red-legged co-occurring with grey partridge. The sum (per half-hour) was then standardised by the number of trials performed on that given lag. Seasonal effect was controlled by considering time (GMT) relative to sunrise (for points in morning) or sunset (evening). To compare distributions of the territorial response across the four modalities, we performed Cramér-von Mises distribution tests.

Within species ecological niches were analyzed with data from 2013-2017, averaging environmental layers across years for each pixel. Three modalities were considered for partridges occurrences (2013-2017): (1) occurrence of only grey partridge (at least once) in the pixel over the 5 years; (2) occurrence of only red-legged partridge; (3) grey and red-legged partridge co-occurring, each being recorded at least once (but not necessarily simultaneously). To compare niche species in absence *versus* co-occurrence with the second species, we used Broennimann et al. (2012) framework. The first step consists in describing the environmental space available in the study area, using the first two axes of a principal component analysis (PCA-env) performed on all pixels with each environmental layers being different variables in the PCA. Then, for each species in each situation (species alone or in co-occurrence), a smoothed density of occurrences is obtained using a kernel density function. Finally, the smoothed densities of occurrence are projected onto the PCA-env space to delineate the niche space for each species in each situation. Niche overlap can then be calculated (e.g. between grey alone and grey co-occurring with red-legged partridge), using Schoener's D index (Warren, Glor, Turelli, & Funk, 2008) which ranges from 0 (no overlap) to 1 (full overlap). In addition, two niche randomization tests can be performed (Broennimann et al., 2012;

Warren et al., 2008). In the niche equivalency test, the two datasets of occurrence are mixed, and two new datasets are constituted randomly (1000 times), conserving the sizes of the two original datasets. The distributed of the 1000 D values of overlap between niches from the paired simulated datasets are compared with the observed value of D: if the latter is outside the range of 95 % of the simulated values, the null hypothesis is rejected, i.e. observed niches are less equivalent than expected by chance (Broennimann et al., 2012; Warren et al., 2008). The similarity test is less conservative, and tests whether the two observed niches (i.e. the gridded density of occurrences in the environmental space) are more similar to each other than to a random niche (Broennimann et al., 2012). One of the observed niches is randomly shifted (i.e. the core of the density of occurrence is randomly placed among the range of available environments), and the overlap with the second one is assessed as a simulated D value. This process is replicated 1000 times. The null hypothesis that a niche is no more similar to the other one than expected at random is rejected if the observed D is greater than 95% of the simulated D values.

Results

Territorial behaviour

Among the 490 surveyed points (cumulating both study sites and years), 21 and 106 points (respectively 2016 and 2017) returned the occurrence of at least one species in at least one of the four sampling sessions. Assuming that the presence of an individual in at least one sampling session for a given point count reflected the presence of a territorial pair, 37 points (7.5%) with grey partridge, 74 (15.1%) with red-legged partridge and 16 (3.3%) with both species were available. We found that grey partridge territorial response was significantly influenced both by the broadcasted species and whether red-legged partridge co-occurred (Table 1a): they responded more to the conspecific than heterospecific call or to the control call (Table S3a). However, co-occurrence with red-legged partridge significantly impaired grey partridge response (Table S3a). Similarly territorial responses of red-legged partridge, when alone, increased to the conspecific song compared to grey partridge's call or control (Table 1b and Table S3b); conversely to grey partridge however, red-legged increased (though non significantly) its response to grey partridge when co-occurring with it while in the same time decreased its response to conspecific, resulting in equal response to any species (Table S3b).

Table 1 Results of GLMMs (Link = binomial, logit) considering the territorial response (vocal behaviour and / or approaches) of grey (a) and red-legged (b) partridges as response variable. Explanatory variables are the Broadcasted songs (*control*, grey partridge, red-legged partridge) and the co-occurrence with the 2nd partridge species (*Alone*, Co-occurrence). Modalities in italics are considered as reference. All models include the playback *sequence* (n=6) and the *rank* (n=2) of the partridge broadcasted songs (grey partridge or red-legged partridge broadcasted first) as random effect.

Variable	χ^2 -value	df	P-value	Estimate $\pm$ SE	Variance of random effects
(a) Grey partridge					
				(intercept: -3.08 ± 0.37)	<i>Sequence</i> : <0.001 <i>Rank</i> : 0.112
Broadcasted song x occurrence of the 2 nd species	0.696	2	0.706		
Broadcasted song	52.235	2	<0.001	(see Table S3a for multiple comparisons)	
Occurrence of the 2 nd species	12.880	1	<0.001	Co-occurrence: -0.839 ± 0.246	
(b) Red-legged partridge					
				(intercept: -3.218 ± 0.476)	<i>Sequence</i> : 0.028 <i>Rank</i> : 0.099
Broadcasted song x occurrence of the 2 nd species	7.714	2	0.021	(see Table S3b)	
Broadcasted song	19.404	2	<0.001	(see Table S3b)	
Occurrence of the 2 nd species	0.444	1	0.505		

Territorial behavior in response to playback alone could discriminate between situations when grey partridges were alone or co-occurring with red-legged, as 92% and 37.5% of points were correctly assigned to their respective category by the LDA (Table 2). Territorial response rate, calling behaviour and territoriality score were the three highest contributive variables discriminating territorial behaviour between the two situations (Fig 2). Grey partridge reduced significantly its response rate and number of calls, and decreased the intensity of territorial response (i.e. territorial score) in areas of co-occurrence (ANOVA, Table S4). These results suggested a shift in the territorial behaviour of grey partridge in co-occurrence situation (Fig. 2a). Conversely, behavioural variables were very poor contributors in discriminating situations where red-legged were alone or co-occurring with grey partridges, with respectively 100% and 0% correctly assigned situations (Table 2, Fig. 2d). Indeed no significant differences appeared for any of the four behavioural variables in the red-legged partridge responses (ANOVA, Table S4), indicating no such shift in behavior in red-legged partridge depending on whether it co-occurred or not with grey partridge (Fig. 2c).

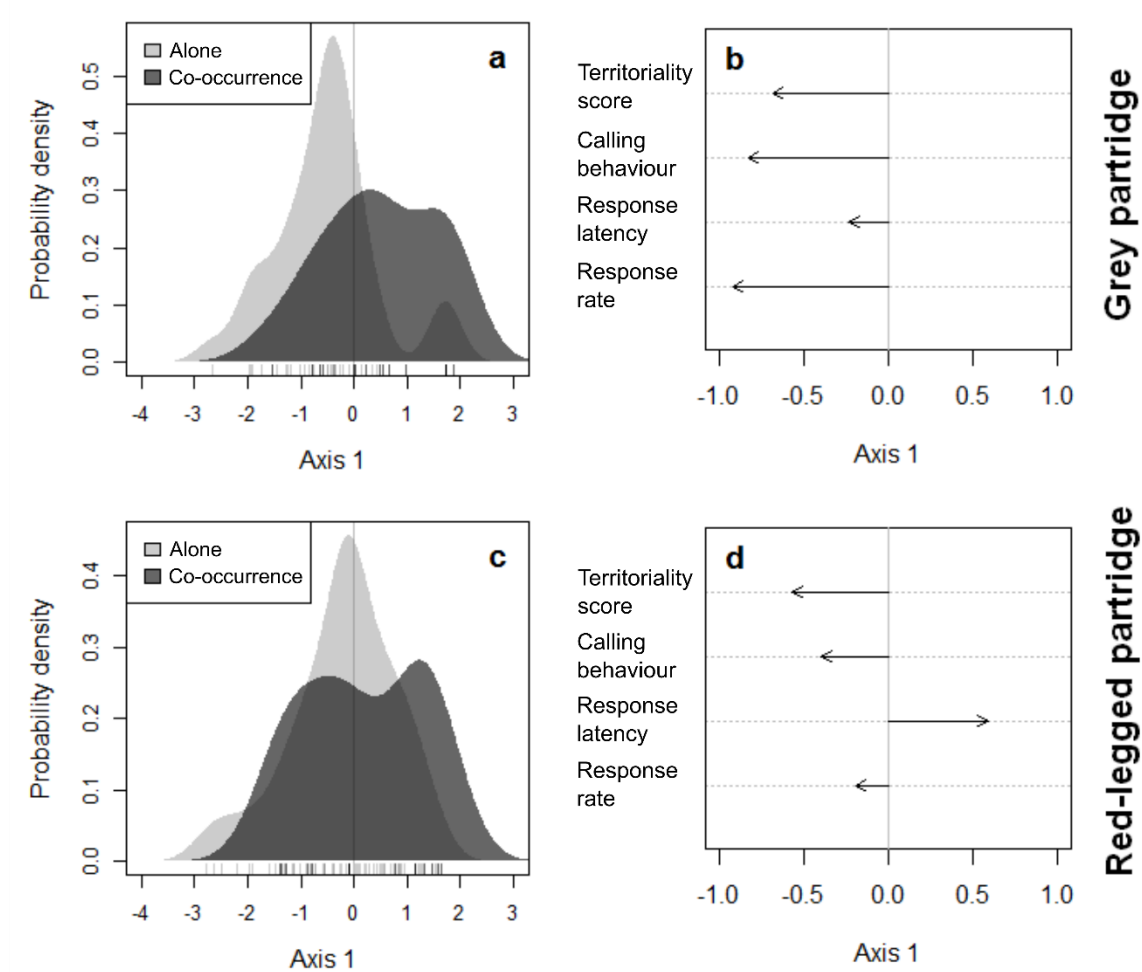


Figure 2 Comparison of territorial behaviours of grey (top) and red-legged (bottom) partridges where alone (light-grey) or in co-occurrence areas (dark-grey). Four behavioural metrics are considered: *territorial response rate*, *calling behaviour*, *response latency* and *territoriality score* (see Table S2 in Appendix A for more details). (a) and (c) show the distribution of the Linear Discriminant Function for grey and red-legged partridges, respectively. (b) and (d) show the correlations in the first dimension (first axis), of the four variables.

Table 2 Results of the cross validation of the Linear Discriminant Analyses carried out on grey (a) and red-legged (b) partridges. The observed number of sampling points in each situation (Alone, Co-occurrence) are represented in rows, and the inferred number of points from the LDAs are presented in columns. For each situation (alone, co-occurrence), the percentage of correct attributions is calculated as the number of sampling points of a given situation well predicted by the discriminant function, divided by the total number of points observed in this situation.

Species	Observed situations	Predicted situations		Correct attributions
		Alone	Co-occurrence	
(a) Grey partridge				
	Alone	34	3	92% (34/37)
	Co-occurrence	10	6	38% (6/16)
(b) Red-legged partridge				
	Alone	74	0	100%
	Co-occurrence	16	0	0%

Daily pattern of grey partridge territorial behaviour was significantly affected by the co-occurrence with red-legged partridge (Fig. 3, Table S5, Appendix A): when alone, grey partridge response was uniform in relation to hour, while its territorial response was lower and restricted around the sunset in the evening in co-occurring situations (Fig. 3). A similar pattern was detected for red-legged partridge where alone *versus* in co-occurrence with grey partridge (Fig. 3, Table S5).

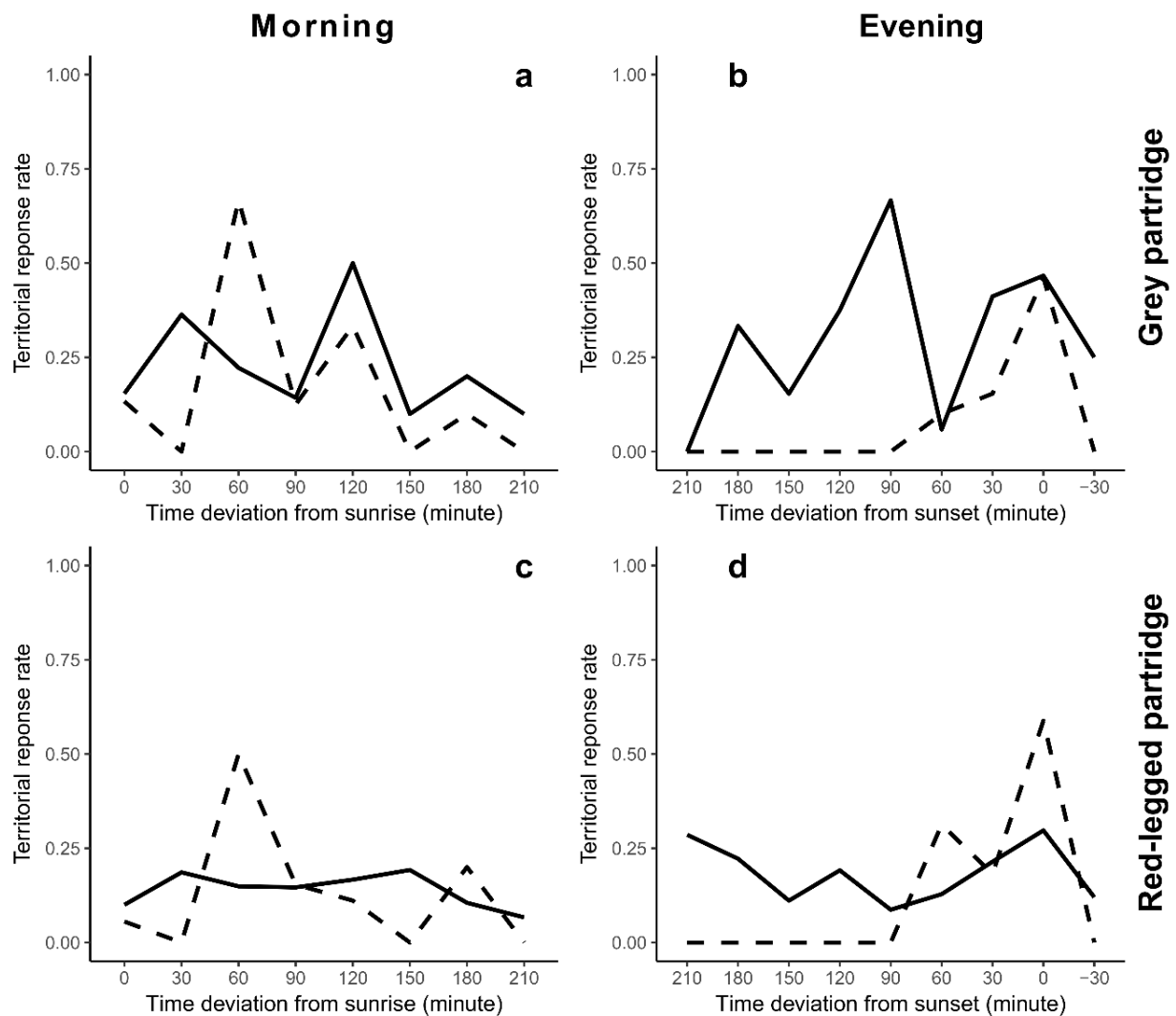


Figure 3 Daily distribution of the territorial response rate of grey (top) and red-legged (bottom) partridges according to the morning time deviation from sunrise (left) and evening time deviation from sunset (right), assessed by playback experiment in 2016 and 2017. Solid lines represent the response rate of each species where alone, dashed lines the response rate where both species co-occurred.

Ecological niche

Grey partridge ecological niche when alone or co-occurring with red-legged partridge overlapped by only 53 % (Fig. 4a compared to 4c), indicating that grey partridge's niche significantly shifted in the presence of red-legged partridge. The equivalency test was significant ($p = 0.02$), indicating that niches are not equivalent: indeed, the core of the grey partridge's niche was shifted in the opposite direction of the red-legged partridge's niche (Fig. 4c), towards greater proportions of spring crops, cereals and rape (Fig. 4e). The non-significance of the similarity test ($p = 0.08$) confirms that niches were no more similar to each other than to a random niche, though the quasi significance suggests that the shift was moderate. Red-legged partridge's niche was wider, composed by preferred open arable land (e.g. spring crops, cereals and rape) but also avoided habitats (woodlands and buildings, Fig. 4e). Conversely to grey partridge, red-legged partridge ecological niche when alone or co-occurring with grey legged partridge showed more overlap (67%, Fig. 4b, d). When co-occurring with grey partridge, red-legged niche did not shift and remained equivalent (equivalency test, $p = 0.55$) and more similar than expected by chance (similarity test, $p = 0.04$).

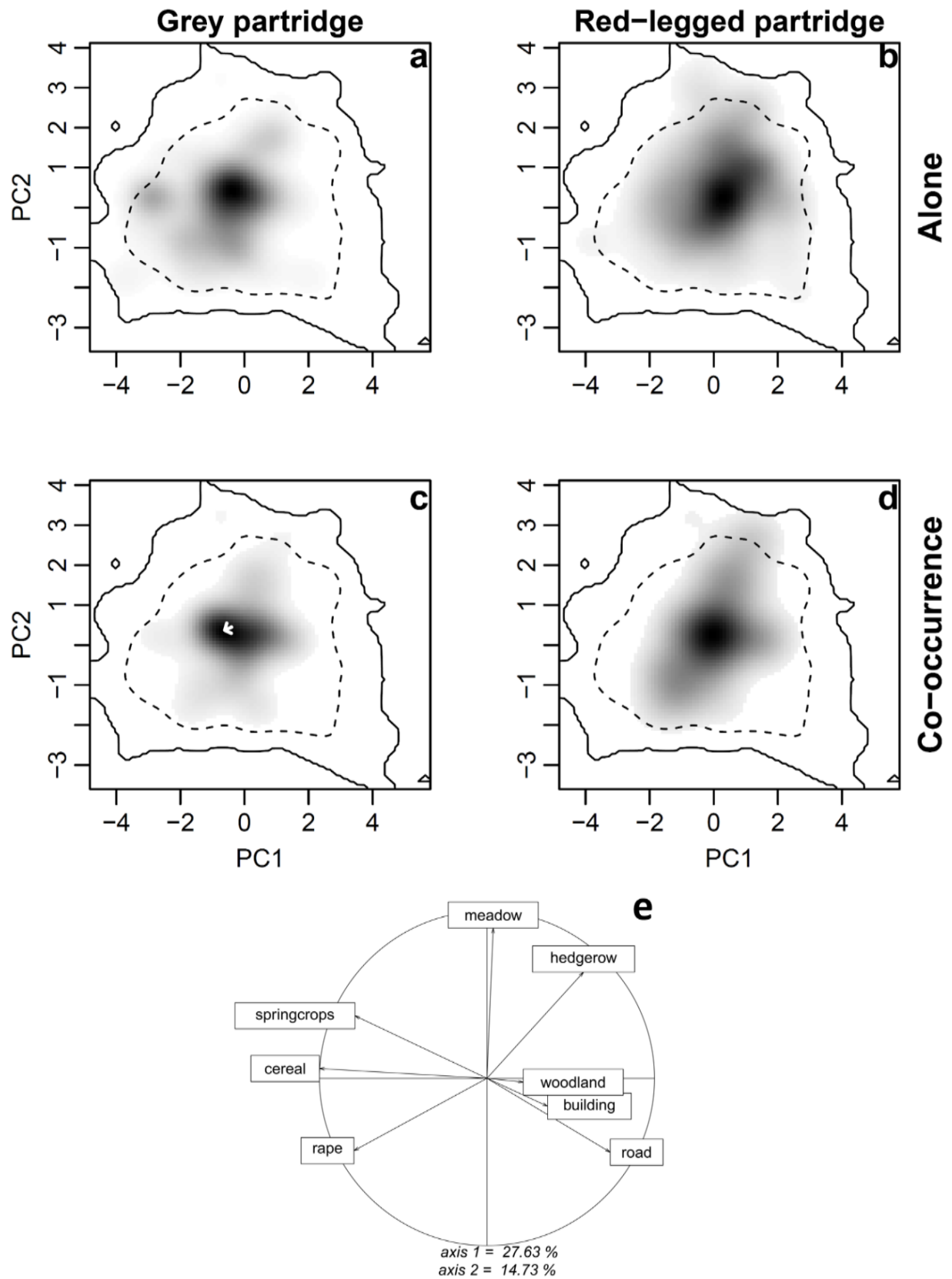


Figure 4 Ecological niche of grey (a) and red-legged (b) partridges when alone and in co-occurrence with the other species (c, d respectively). A white arrow materializes a significant shift of the niche centroid in presence compared to absence of the second species. (e) represents the correlation circle of the PCA describing the environmental space available in the study area.

Discussion

Our results confirm an asymmetric pattern of territorial competition behaviour between grey and red-legged partridges, occurring through an impaired territorial response and behavioural phenology of grey partridge when co-occurring with red-legged partridge, associated with asymmetric outcomes in ecological niches. In co-occurrence areas, grey partridge territorial behaviour was of lower intensity toward heterospecific call than to conspecific. Such shifts in territorial behaviour intensity when facing a competitive species towards a more discreet behaviour have already been documented in birds (e.g. Martin & Martin, 2001a; McEntee, 2014) and other vertebrates such as mammals (e.g. Pasch et al., 2013). Indeed in these cases the typical response of the subordinate species is to avoid unfriendly interactions with a dominant and larger competitor. Conversely, the red-legged partridge territorial response rate moved for asymmetric response intensity between conspecific and heterospecific (showing much higher response rate to its own species) when alone, to equal response rates to both species in situations of co-occurrence. Such convergence of territorial behavior has already been documented (Jankowski et al., 2010; Pasch et al., 2013). Such patterns of change in response intensity to heterospecific call in situation of co-occurrence or not actually refutes the hypothesis of Murray (1971) who proposed that interspecific territoriality result from misdirected intraspecific interactions due to misleading signal recognition. We also found that both species adjusted their daily territorial activity in situation of co-occurrence with the other species, though overall territorial activity pattern of both species remained synchronized and was not segregated in time. This unexpected result may be explained by a potentially too coarse temporal resolution in our analyses, making temporal shifts in territorial response hard to detect. Indeed Brumm (2006) demonstrated that Nightingale *Luscinia megarhynchos* B. 1831 adjusts its vocal activity by calling within the silent intervals between two heterospecific broadcasted songs. Finally, we detected slight habitat niche shift in the less competing species in situations of co-occurrence with the dominant species, while there was no such shift for the dominant species, underlying asymmetric pattern of competition for habitat likely resulting from the aggressive behaviour (e.g. Jankowski et al., 2010; Martin & Martin, 2001b, 2001a). Grey partridge (the subordinate species) niche shifted to more open habitats, which could be more subjected to disturbance therefore poorer-quality breeding habitat, likely promoting lower fitness expectancy (see Martin et al., 2017; Martin & Martin, 2001b, 2001a).

Asymmetric competition occurring in the contact zone of parapatric species is well-known to impair the fitness of the subordinate species (Jankowski et al., 2010; Martin & Martin, 2001a). Therefore, huge releases of red-legged partridges in the core area of grey partridge, which resulted in an artificial increase in the contact zone between species, raises concerns not only for grey partridge decline but also for its future possible recovery. This is because the presence of morphologically similar species has long been identified as interfering with the re-establishment success in translocations (Griffith, Scott, Carpenter, & Reed, 1989). Grey partridge is indeed a species of focus interest for many supplementation or reinforcement projects, identified as the only tool for restoring self-sustainable populations in many areas (Buner & Aebischer, 2008; Buner, Browne, & Aebischer, 2011). Our study thus suggests that the presence of red-legged partridges may limit the chances of success in such projects. Releasing non-native species has long been used as a strategy to limit hunting pressure on wild native populations (Aebischer & Ewald, 2004; Bro, 2016; Carpio et al., 2017). However this has proved inefficient in grey partridge (Reitz, 2003), or even counterproductive, because of reverse effects such as overshooting caused by inadvertent shots (Aebischer & Ewald, 2004), indirect competition for resources with common pheasant *Phasianus colchicus* L. 1758 (Renzoni, 1974), parasites introduction leading to parasite-mediated competition with pheasant and niche exclusion (Tompkins, Draycott, & Hudson, 2000; Tompkins, Greenman, & Hudson, 2001; Tompkins, Greenman, Robertson, & Hudson, 2000), or pheasants laying eggs into grey partridge nests (Robertson, 1996). Given repeated failures in gamebird supplementation programs to restore self-sustainable populations (see Sokos et al., 2008), we plea for more integrative, ecologically coherent and viable schemes. This includes some funding reallocation towards habitat improvement in order to decrease competition pressure, and a more meticulous examination of the species to release according to ecology and natural ranges. Furthermore, our study highlights the importance of accounting for the presence of ecologically, phylogenetically or morphologically close species (Griffith et al., 1989), as a potential major limitation of reintroduction programs (see also IUCN Species Survival Commission, 2013).

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Supporting information

Appendix A. Supporting information and results to the main text

Table S1 Grey and red-legged partridge density estimations (mean $\pm$ SD) in the Long-Term Socio-Ecological Research site “Zone Atelier Plaine & Val de Sèvre” (LTSER ZAPVS) and the Maine-et-Loire study area (METL) in 2017. Estimations were realized from playback experiment of 2016 and 2017.

Species	Density in the LTSER ZAPVS	Density in the METL study area
Grey partridge	0.25 ($\pm$ 0.07)	0.49 ($\pm$ 0.20)
Red-legged partridge	0.15 ($\pm$ 0.09)	2.62 ($\pm$ 0.54)

Table S2 Description of behavioural variables considered in the analysis of territorial behaviour, and predictions under a hypothetic asymmetric competition for the dominant and subordinate species. Metrics were calculated for each species, on each point count.

Behavioural metric	Description	Prediction
Territorial response intensity	The sum of responding individuals (by approach and or vocalization) controlled by the number of expected responses (number of individuals seen on this point).	In co-occurrence areas, we expected a higher territorial response intensity for the dominant species, and a lower for the subordinate one (see Jankowski et al., 2010; and Martin & Martin, 2001a)
Response latency	The mean response latency (i.e. the time spent between the beginning of the broadcasted song and the vocal response) recorded over the 4 sampling sessions.	In co-occurrence area, the response latency is expected to be lower for the dominant species, higher for the subordinate (see Jankowski et al., 2010; and Martin & Martin, 2001a)
Calling behaviour	The mean number of song responded by individuals, among the conspecific and heterospecific partridge songs. Ranges from 0 (any individual responded to partridges' songs over the four sampling sessions), to 2 (all individuals responded to the two partridge songs at each of the four sessions).	Expected to be high for a dominant species responding as well as conspecific than heterospecific song, while it is expected to be low for a subordinate species not responding to the heterospecific song (Martin & Martin, 2001a).
Territoriality score	The mean of the territoriality score obtained by each individual over the four sampling sessions, following the ranking of increasing territoriality: 0 – no response, 1 – approach, 2 – vocalization, 3 – approach with vocalization, 4 – flying approach with vocalization.	We expected that the dominant species demonstrate a higher territoriality score in co-occurrence with the subordinate one, while the reverse was expected for the subordinate species (see Jankowski et al., 2010; and Martin & Martin, 2001a)

Table S3 Tukey's multicomparison post-hoc tests computed after GLMMs (Link = binomial, logit) performed on the territorial response of grey (a) and red-legged (b) partridge species as response variable, and considering the broadcasted species song (grey partridge, red-legged partridge, and common quail as control), and to the co-occurrence with the 2nd partridge species (Alone, co-occurrence).

Variable	Estimate	SE	z-ratio	p-value
(a) Grey partridge				
Grey partridge – Red-legged partridge	1.161	0.246	4.722	<0.001
Grey partridge – Common quail	1.822	0.305	5.970	<0.001
Red-legged partridge – Common quail	0.662	0.341	1.939	0.125
(b) Red-legged partridge				
Red-legged partridge, Alone – Grey partridge, Alone	1.007	0.245	4.118	<0.001
Red-legged partridge, Alone – Common quail, Alone	0.926	0.238	3.882	0.001
Red-legged partridge, Alone – Grey partridge, Co-occurrence	0.335	0.319	1.050	0.901
Red-legged partridge, Alone – Common quail, Co-occurrence	1.159	0.437	2.656	0.084
Red-legged partridge, Alone – Red-legged partridge, Co-occurrence	0.732	0.368	1.988	0.349
Red-legged partridge, Co-occurrence – Grey partridge, Alone	0.275	0.399	0.687	0.983
Red-legged partridge, Co-occurrence – Common quail, Alone	0.193	0.396	0.489	0.997
Red-legged partridge, Co-occurrence – Grey partridge, Co-occurrence	-0.397	0.448	-0.885	0.950
Red-legged partridge, Co-occurrence – Common quail, Co-occurrence	0.427	0.538	0.793	0.968
Grey partridge, Alone – Common quail, Alone	-0.081	0.284	-0.286	1.000
Grey partridge, Alone – Common quail, Co-occurrence	0.152	0.463	0.329	0.999
Grey partridge, Alone – Grey partridge, Co-occurrence	-0.671	0.355	-1.893	0.387
Grey partridge, Co-occurrence – Common quail, Alone	0.590	0.351	1.684	0.522
Grey partridge, Co-occurrence – Common quail, Co-occurrence	0.824	0.506	1.628	0.559
Common quail, Alone – Common quail, Co-occurrence	0.234	0.460	0.508	0.995

Table S4 Effect of the independent variable co-occurrence of the 2nd species (*Alone*, Co-occurrence) on the territorial behaviour of grey (a), and red-legged (b) partridges, considered as four dependent variables: territoriality score, response latency, calling behaviour, territorial response rate (see Table S2 for more details). The modality in italic was taken in reference in models.

Species	Dependent variables	Independent variables	t- value	df	P-value	Estimate ± SE
(a) Grey partridge	Territoriality score	(intercept)	8.013	1	<0.001	(4.270 ± 0.533)
		co-occurrence of the 2 nd species	-2.212	1	0.032	Co-occurrence: -2.145 ± 0.970
	Response latency	(intercept)	7.337	1	<0.001	(194.720 ± 26.540)
		co-occurrence of the 2 nd species	-0.733	1	0.467	
	Calling behaviour	(intercept)	12.118	1	<0.001	(1.284 ± 0.106)
		co-occurrence of the 2 nd species	-2.741	1	0.008	Co-occurrence: -0.529 ± 0.193
	Territorial response rate	(intercept)	14.044	1	<0.001	(0.255 ± 0.018)
		co-occurrence of the 2 nd species	-3.098	1	0.003	Co-occurrence: -0.102 ± 0.033
(b) Red-legged partridge	Territoriality score	(intercept)	10.179	1	<0.001	(2.095 ± 0.206)
		co-occurrence of the 2 nd species	-0.781	1	0.437	
	Response latency	(intercept)	9.042	1	<0.001	(194.550 ± 21.520)
		co-occurrence of the 2 nd species	0.794	1	0.429	
	Calling behaviour	(intercept)	8.966	1	<0.001	(0.718 ± 0.080)
		co-occurrence of the 2 nd species	-0.543	1	0.589	
	Territorial response rate	(intercept)	10.900	1	<0.001	(0.174 ± 0.016)
		co-occurrence of the 2 nd species	-0.267	1	0.790	

Table S5 Cramer – von Mises' distribution tests comparing the territorial response rate of (a) grey and (b) red-legged partridges in single-species *versus* co-occurring situations. Periods of the day (morning, evening) were analyzed separately.

Species	Period	T	P-value
(a) Grey partridge	Morning	0.108	0.274
	Evening	0.445	0.019
(b) Red-legged partridge	Morning	0.116	0.165
	Evening	0.306	0.008

Appendix B. Preparation of playback sequences and origin of the broadcasted songs

Each audio sequence contained three phases, corresponding to the territorial song of grey partridge, red-legged partridge and Common quail (Table S6). For each species, the audio phases were prepared to last around 155 seconds by repeating calls from at least three different individuals (Table S7), to avoid intimidation of too much territorial calls (Novoa, 1992). In each audio sequence, species phases were separated by 1 minute of silence. Audio sequence were randomly displayed, yet making sure that grey partridge's song was displayed as the first song of the sequence at least once (morning or evening) on each survey point.

Table S6 Six orders of arrangement of broadcasted songs according to the sequence prepared.

Sequence number	1 st species	2 nd species broadcasted	3 rd species broadcasted
1	Grey partridge	Red-legged partridge	Common quail
2	Grey partridge	Common quail	Red-legged partridge
3	Common quail	Grey partridge	Red-legged partridge
4	Common quail	Red-legged partridge	Grey partridge
5	Red-legged partridge	Common quail	Grey partridge
6	Red-legged partridge	Grey partridge	Common quail

Table S7 Origin of songs used to prepare audio sequences for grey partridge, red-legged partridge and Common quail.

Species	Song position	Author	Source	File name	Date	Time	Country
Grey partridge	1 st and 2 nd songs	Jean C. Roché	<i>Oiseaux d'Europe et du Maghreb (CD)</i> ¹	Perdrix grise.mp3	-	-	-
	3 rd song	Krzysztof Deoniziak	xeno-canto ²	XC247485	01/06/2015	21:00	Poland
	4 th song	Peter Boesman	xeno-canto ²	XC280950	28/05/2008	06:50	Belgium
	5 th song	David M.	xeno-canto ²	XC288385-T05	08/01/2012	07:19	UK
Red-legged partridge	1 st song	Jean C. Roché	<i>Oiseaux d'Europe et du Maghreb (CD)</i> ¹	Perdrix rouge.mp3	-	-	-
	2 nd song	David M.	xeno-canto ²	XC284092	25/04/2013	21:03	UK
	3 rd song	David M.	xeno-canto ²	XC197092-T02	03/07/2013	20:53	UK
Common quail	1 st song	Jean C. Roché	<i>Oiseaux d'Europe et du Maghreb (CD)</i> ¹	Caille des blés.mp3	-	-	-
	2 nd song	Cedric Mrozko	xeno-canto ²	XC256801	03/07/2015	15:00	Portugal
	3 rd song	Piotr Szczypinski	xeno-canto ²	XC252505	12/06/2015	07:30	Poland
	4 th song	Peter Boesman	xeno-canto ²	XC280955	26/05/2007	11:15	Belgium
	5 th song	Tomas Belka	xeno-canto ²	XC80610	27/05/2015	14:00	Portugal
	6 th song	vprannila	soundcloud ³	Viiriäinen	25/05/2015	-	Finland

¹ Roché, J.C. (2001). *On Oiseaux d'Europe et du Maghreb* [CD]. Sittelle-Ceba.

² Xeno-canto Foundation, & Naturalis Biodiversity Center. (2005). Xeno-canto Partager les sons d'oiseaux du monde entier. Retrieved February, 2016, from <http://www.xenocanto.org/>

³ SoundCloud Limited. (2016). SoundCloud. Retrieved February, 2016, from <https://soundcloud.com/>

Appendix C. Estimation of the sampling error

We assessed the sampling error as the proportion of point counts considered as free of a partridge species while the species is present but not detected. To do this, we realized a rarefaction analysis under the PAST software (Hammer, Harper, & Ryan, 2001).

For each species, we first drew the cumulative curves of point counts where species was detected as function of the rank of the sampling session (Fig. S1). The rarefaction curves revealed that our sampling is not exactly exhaustive as the plateau is not reached.

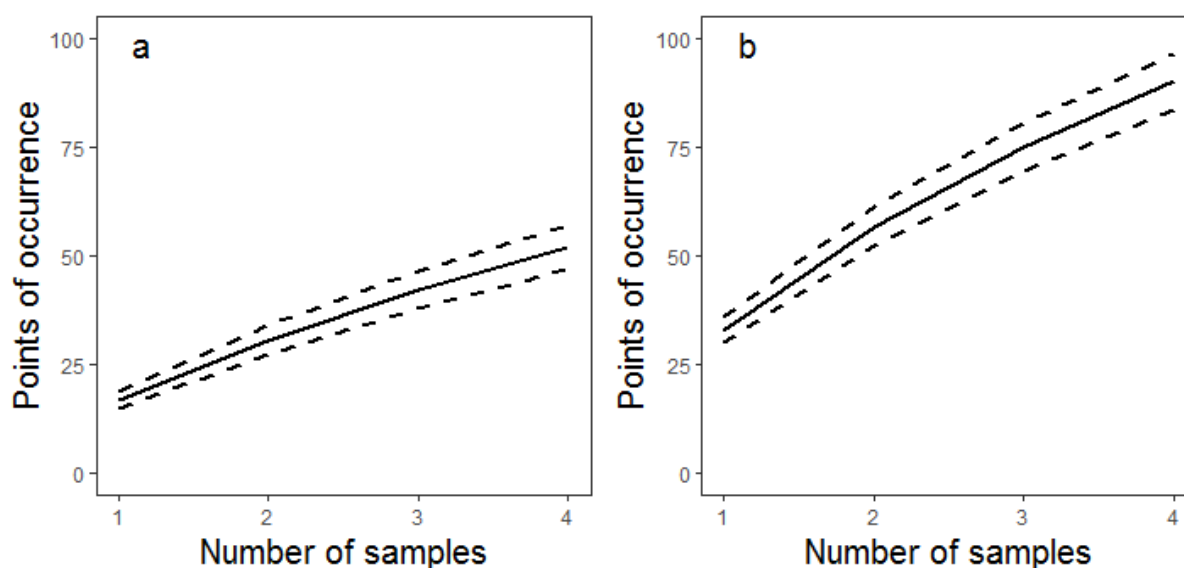


Figure S1 Cumulated number of point counts with occurrence of (a) grey partridge, (b) red-legged partridge, as a function of the number of the sampling session. Dashed lines correspond to 95% confidence intervals.

Then we estimated the total number of point counts expected to host each species (Table S8). As several estimators can be used to do this, we run four estimators and then averaged them to obtain a synthetic index. This analysis revealed that on average 85 point counts may host grey partridge and 140 may host red-legged partridge (Table S8).

Table S8 Estimation of the expected number of point counts hosting grey and red-legged partridges according to the richness estimator.

Richness estimator	Grey partridge	Red-legged partridge
Chao 2	98.313	156.375
Jackknife 1	81.250	135.000
Jackknife 2	97.083	158.667
Bootstrap	65.031	110.211
<i>Mean of estimations</i>	<i>85.419</i>	<i>140.063</i>

Finally, we calculated the proportion of false negative point counts (i.e. the species is present but not detected) according to the following function (Table S9):

$$\frac{\text{Number of false negative points}}{\text{Number of observed negative points}} * 100$$

$$= \frac{\text{Estimated number of occurrence points} - \text{Observed number of occurrence points}}{\text{Total number of sampled points} - \text{Observed number of occurrence points}} * 100$$

Therefore, we can consider that the sampling error is about 7.3% for the grey partridge and 12.5% for the red-legged partridge (Table S9).

Table S9 Sampling error calculated as the percentage of false negative point counts (i.e. the proportion of points considered as free of partridge while the species is present but not detected).

	Grey partridge	Red-legged partridge
Total number of sampled points	490	490
Observed number of points with a species occurrence	53	90
Estimated number of points with species occurrence	85	140
Proportion of false negative points	7.3%	12.5%

Chapitre III

*Ajustements de la sélection de l'habitat au
cours du cycle circadien : une réponse à la
spatio-temporalité des perturbations naturelles
et humaines ?*

Avant-propos et résumé du Chapitre III

Le risque de prédation et le dérangement humain sont des processus écologiques structurés dans l'espace et dans le temps, qui façonnent les mouvements des animaux (minimisation du risque) et affectent les dynamiques de populations. La compréhension de la périodicité des mouvements au cours du cycle circadien est donc cruciale en gestion des populations pour identifier l'ensemble des pressions environnementales contraignant ces populations.

Alors que plusieurs études révèlent une sélection (ou un évitement décroissant) diurne chez la Perdrix grise d'éléments paysagers associés à un fort risque de prédation par les carnivores (voir Chapitre I), dont l'activité est principalement nocturne, peu d'études se sont intéressées à la capacité d'ajustement comportemental de la Perdrix grise face à la temporalité des perturbations auxquelles elle est confrontée : activités humaines dans les parcelles la journée (agriculture, chasse) et risque de prédation par les carnivores élevé la nuit.

Dans ce Chapitre III, à partir d'un suivi individuel de Perdrix grises équipées de GPS, nous analysons les ajustements comportementaux (activité, utilisation de l'espace, sélection de l'habitat) de la Perdrix grise au cours du cycle circadien, et proposons des mécanismes explicatifs liés à la variation temporelle des perturbations (risque de prédation, chasse).

Nos résultats montrent des pics d'activité de déplacement à l'aube et au crépuscule, probablement expliqués par des mouvements entre sites diurnes et nocturnes (distants d'environ 330 m), caractérisés par des habitats différents (sélection de végétation rase/absente et évitement des réservoirs de prédateurs – boisements et zones bâties – la nuit *versus* une utilisation plus importante des couverts à végétation haute la journée tels que les boisements et le maïs). Des différences dans l'utilisation de l'espace ont également été observées entre survivants et non-survivants : les oiseaux prédatés étaient plus près des routes, les oiseaux chassés plus loin des haies la journée, que les survivants. Les non-survivants avaient également un taux de diffusion de leur site de lâcher plus faible que les survivants.

Cette étude identifie la prédation et la chasse comme pressions de sélection complémentaires, sélectionnant les oiseaux sur la base de leurs comportements d'utilisation de l'espace et de sélection de l'habitat, qui façonneraient les comportements spatiaux au niveau de la population. Les implications pour la gestion cynégétique sont discutées et nous suggérons une meilleure considération et minimisation des pressions environnementales survenant tout au long du cycle circadien pour une gestion efficace de la faune sauvage.

Changes in spatial behaviour of the grey partridge *Perdix perdix* along the diel cycle: a response to the spatiotemporal structuration of natural and human disturbances?

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Abstract

Heterogeneous landscapes constrain animals to move to meet suitable habitats while avoiding unfriendly interactions. Predation risk and human disturbances are well-known spatiotemporally structured ecological processes shaping animal movements, with outcomes on population dynamics that could overpass effects of direct mortality. Understanding periodicity of animal movements along the diel cycle is crucial, to identify periodic pressures constraining populations.

We investigated patterns of activity, space use and habitat selection and causes for variations along the diel cycle for the grey partridge *Perdix perdix*, a declining archetypal farmland species, threatened by predation. We used individual-based GPS locations acquired from a post-release monitoring of captive-reared birds (2015-2018). We first modeled movement activity and analyzed habitat selection along the diel cycle. We then investigated differences in space use patterns (i.e. distance to risky landscape features, distances travelled after nocturnal disturbances, diffusion from the release site) according to the fate of birds (predated, hunted or survivors).

We detected peaks of activity around dawn and dusk, likely explained by commuting movements between diurnal and nocturnal sites composed by different habitats (selection of

short-vegetation covers and avoidance of predator reservoirs at night *versus* higher use of high-vegetation covers during daytime). Differences in space use were also detected between survivors and non-survivors: predated birds were closer to roads than survivors, while hunted birds were farther from hedgerows during daytime. Non-survivors (predated and hunted) had lower diffusion from their release site than survivors.

This revealed predation and hunting activity as contrasting selection pressures in agricultural landscapes, selecting birds on the basis of their space use and habitat selection behaviours. Associated with their non-lethal effect (i.e. disturbances), these environmental pressures would have probably shaped the temporal adjustments in space use and habitat selection behaviours observed at the population scale. This raises concerns about game management through releases of birds during periods of high disturbances (before harvesting crops, hunting season), and we suggest to reconsider this practice to ensure the population maintenance or recovery. We further plea for a better consideration and minimization of environmental pressures and disturbances along the diel cycle to reliably identify factors constraining populations for efficient conservation or wildlife management.

Key-words

Activity patterns, Commuting behaviour, Global Positioning System, Grey partridge, Habitat selection, *Perdix perdix*, Predation risk, Space use

Introduction

In heterogeneous landscapes, because of the patchy distribution of resources, animals are constrained to move to fulfill their daily biological requirements (Barraquand & Benhamou, 2008). The best places for foraging are not necessarily the safest places for resting or profitable places to carry out all daily activities (see Barraquand & Benhamou, 2008; Cornélis et al., 2011; Mueller, Selva, Pugacewicz, & Prins, 2009). Therefore, understanding the temporality of animal activity and movements is fundamental, resulting from environmental pressures shaping individual behaviours and population dynamics (Béchet, Giroux, & Gauthier, 2004; Creel & Christianson, 2008; Creel, Christianson, Liley, & Winnie, 2007; Gaynor, Hojnowski, Carter, & Brashares, 2018). Considering the use of space by animals along the whole circadian cycle is thus of prior concern to reliably address ecological processes involved in space and habitat uses (Kochanny, Delgiudice, & Fieberg, 2009; Sirot, Renaud, & Pays, 2016). However, the focus on the nocturnal period in diurnal birds species remains limited (e.g. Jirinec, Varian, Smith, & Leu, 2016; Ward, Alessi, Benson, & Chiavacci, 2014), despite the rise of Global Positioning System (GPS) telemetry enabling high resolution monitoring (Cagnacci, Boitani, Powell, & Boyce, 2010; Tomkiewicz, Fuller, Kie, & Bates, 2010).

Ecological processes shaping animal movements may vary over space and time. Among them, predation risk is a dynamic process (e.g. Creel, Winnie, Christianson, & Liley, 2008; Creel, Winnie, Maxwell, Hamlin, & Creel, 2005; Fortin et al., 2005), whose outcomes on the prey behaviour and population dynamics can overtake direct effects of predation (Creel & Christianson, 2008; Preisser, Bolnick, & Benard, 2005). For instance, some prey respond to a higher predation risk at night by adjusting their patterns of activity toward a lower activity at night and a higher activity at dawn and dusk or during the day (e.g. Roth & Lima, 2007; Webb, Gee, Strickland, Demarais, & DeYoung, 2010). Prey species may also modify their patterns of space and habitat use toward lower-risk areas and habitats (Creel et al., 2005; Fortin et al., 2005). In human-dominated landscapes, human daytime activity (e.g. agricultural field work, outdoor recreational activities) also contribute to shape the wildlife behaviour (Banks & Bryant, 2007; Gaynor et al., 2018; Pan et al., 2011), which could induce energetic costs (Arlettaz et al., 2015; Béchet et al., 2004) and affect demography (Liley & Sutherland, 2007; Stillman, West, Caldow, & Durell, 2007), in a comparable way than predation risk (Ciuti et al., 2012; Frid & Dill, 2002). Consequently, understanding the periodicity of animal activity, space

and habitat use is of prior concern for wildlife management and conservation, to identify the periodic pressures constraining populations (Riotte-Lambert, Benhamou, & Chamaillé-Jammes, 2013; Tolon et al., 2009).

Grey partridge *Perdix perdix* L. 1758, one of the most archetypal farmland gamebird in Europe (Sotherton, Aebischer, & Ewald, 2014), is now considered of conservation concern due to the widespread decline it has accused for 70 years (Eaton et al., 2015; Hayhow et al., 2017), mainly imputed to agricultural intensification (Aebischer & Potts, 1994). In the recent phase of the decline, the increased predation pressure on the few remaining suitable habitats has become one of the main threat to the already weakened populations (Aebischer & Ewald, 2012; Bro, Sarrazin, Clobert, & Reitz, 2000). In Western Europe, predation events on grey partridge mainly involve carnivores as Red fox *Vulpes vulpes* L. 1758, domestic cat *Felis catus* L. 1758, and mustelids (Bro et al., 2013; Bro, Reitz, Clobert, Migot, & Massot, 2001; Buner & Schaub, 2008; Kamieniarz & Panek, 2011). Carnivore activity increases at night (Doncaster & Macdonald, 1997; Horn, Mateus-Pinilla, Warner, & Heske, 2011; Roy, Ghoshal, Bijoor, & Suryawanshi, 2018) and the induced predation risk could be spatially biased near linear features as corridors (roads, hedgerows; Červinka, Šálek, Padyšáková, & Šmilauer, 2013; Reitz & Mayot, 1999), and predator reservoirs (woodlands: Dudzinski, 1992; built-up areas: Putaala, Turtola, & Hissa, 2001; Reitz, Le Goff, & Fuzeau, 2002). Despite, recent studies based on diurnal monitoring documented a selection or low avoidance of such risky landscape features (see Bro, Mayot, Corda, & Reitz, 2004; Harmange, Bretagnolle, Sarasa, & Pays, 2019; Rantanen, Buner, Riordan, Sotherton, & Macdonald, 2010), little is known about the grey partridge capacity of behavioural adjustment to the nocturnal period. Furthermore, some indices suggest that grey partridge may have no activity at night except in response to an obvious disturbance, and use lower-risk areas offering a greater visibility and enabling a better predator detection (see Metcalfe, 1984) (e.g core of fields, short vegetation cover; Tillmann, 2009). Therefore, studies investigating behavioural adjustments in activity and space use patterns along the diel cycle from individual-based data in grey partridge are lacking.

Using individual-based GPS locations, this study explores the grey partridge behavioural adjustment in relation to the spatiotemporal structuration of pressures (i.e. nocturnal predation risk, diurnal human activity). We particularly address the following questions: (i) Are birds able to adjust their patterns of activity, space use and habitat selection along the diel

cycle and to what extent? And if so, (ii) could behavioural adjustments result from a change in spatiotemporal structuration of natural and human disturbances? We first expected changes in grey partridge activity, space use and habitat selection at night towards a lower activity, and areas or habitats associated with low predation risk (avoidance of risky features as hedgerows, roads/tracks, woodlands, built-up areas; selection of short vegetation covers) (see Tillmann, 2009). During daytime, the reverse is expected (selection of high-vegetation covers providing good refuges and food as hedgerows, woodlands, unharvested crops; and an avoidance of open areas and short-vegetation covers) as a result of the avoidance of human activity (agricultural field work and outdoor recreational activities).

Secondly, effects of distances to the nearest linear feature as predator corridors (hedgerow, road or track), and predator reservoirs (woodland, built-up area), were tested on the probability for birds to undertake nocturnal movements (expected to occur exclusively to escape from obvious disturbances; see Tillmann, 2009). Probability to move should decrease with increasing distance to predator-rich features (if nocturnal movements reflect an escape behaviour from a predator attack). On the other hand, we investigated whether predated, hunted, or survivor individuals demonstrated differences in their space use patterns: diurnal and nocturnal distances to predator corridors and reservoirs, distances travelled during nocturnal movement (as proxy of escape distance), and exploration capacity (as a diffusion coefficient, see Pays, Fortin, Gassani, & Duchesne, 2012). Behavioural differences between predated birds and survivors were expected to occur at night, when the predation risk is higher. Predated birds were expected to be closer to linear features at night, and to have lower escape distances than survivors. Conversely, behavioural differences between hunted birds and survivors were expected to occur during daytime, when hunting activity occurs. Hunted birds were expected to be farther from semi-natural permanent refuge covers (e.g. hedgerows) during daytime and should have a lower escape distance.

Material & methods

Study sites

The monitoring was lead from 2015 to 2018, on the Long-Term Socio-Ecological Research (LTSER) platform « Zone Atelier Plaine & Val de Sèvre » Western France. This plain of 435 km² is characterized by an intensive agricultural landscape mainly oriented toward cereal

production. The spring land-cover has been exhaustively surveyed annually from 1994 onwards and was characterized by winter cereals (41.5%), sunflower (10.4%), corn (9.6%), rape (8.3%), meadows (13.5%), woodlands (2.9%) and built-up areas (9.8%) (mean values over the period 2009-2016 in Bretagnolle et al., 2018). The grey partridge density in the study region is low (around 1 male or pair per 400 ha), and maintained through annual releases of captive-reared birds (Bro & Crosnier, 2012; Reitz, 2003). In the LTSEr, the GPS monitoring was led on the extent of the municipal territories of four approved communal hunting societies: Fors, Marigny, Mougou and Prahecq.

Study birds and releasing protocols

A first protocol was conducted during 2015 and 2016 hunting seasons (from late August to mid-November), on the hunting societies of Fors, Mougou and Prahecq, allowing grey partridge shooting. We took the opportunity offered by hunters to tag birds released for hunting purpose with GPS devices. Releasing protocols were thus constrained by little flexibility, compelled by the releasing practices of each hunting society (Table 1). All birds were released prior to hunting season, from late August to early September, by flocks of 15 to 20 birds. Around 60 birds were released per municipality, and either placed in acclimation pens (measuring ca. 5 m²) during 7 to 10 days (Fors and Mougou) or directly hand-released without acclimation phase (Prahecq) (see Table 1). Birds were either released all at the same date (in Prahecq, and in some release sites in Fors and Mougou), or in some pens birds were sequentially released (allowing 2 birds get out of the pen each day, in some release sites of Fors and Mougou).

A second protocol was developed with the hunting society of Marigny, engaged in a third-year suspension of the grey partridge shooting. 131 birds were released in mid-December 2016 and 179 in mid-September and in late October 2017. Birds were released by flocks of 12-16 individuals (50% males and 50% females) with 6-8 individuals tagged. In each site, birds were all released at the same date after a 5-day acclimation phase (or 3-day when predator traces were observed around pens) in pens (of ca. 5 m²).

In both protocols, individuals were measured (weight, wing length, tarsus length), sexed, and tagged by data loggers (CatLog-S2, Catnip Technologies Ltd, Hong Kong) fitted on their breast through a necklace. In the second protocol, birds were fitted either by CatLog, or, for 7

birds, by more performing GPS trackers enabling remote data transmission (5 units of UvA-BiTS GPS-trackers, www.uva-bits.nl, Bouten, Baaij, Shamoun-Baranes, & Camphuysen, 2013; and 2 units of Milsar's GsmRadioTag-S9, www.milsar.com). These devices were fitted on their back through a harness. In this protocol, birds were also ringed by colour and alphanumeric metal gamebird rings.

Table 1 Summary of the number of birds released each year in each approved communal hunting society and the release practices employed.

Hunting society	N of birds tagged (N of males)			Duration of acclimation	Simultaneous release
	2015	2016	2017		
Fors	69 (26)	46 (32)	-	Up to 10 days	No
Mougon	58 (37)	32 (18)	-	Up to 7 days	No
Prahecq	58 (?)	60 (35)	-	0 day	Yes
Marigny	-	63 (57)	66 (32)	3-5 days	Yes

Data collection and preparation

Facing the trade-off between maximization of the battery lifespan and the recording frequency of fixes, in 2015, loggers were programmed to turn-on 1 week before the hunting season onset (the dispersion phase was not captured as birds were already out of pens), and recorded 1 fix / 30 min during daytime and no nocturnal data were recorded. Since 2016, all loggers turned-on at the release time, recorded 1 fix / 15 min during daytime and 1 fix / hour at night (this enabled a lifespan around 1.5-2 months). The 7 GPS transmitters were initially programmed to record 1 fix / 10 min during daytime and 1 fix / 30 min at night, and then remotely reprogrammed at a finer temporal resolution (up to 1 fix / 5 min during daytime and 1 fix / 15 min at night) when battery charge allowed.

As data loggers did not remotely transmit recorded fixes, they had to be recovered. In the first protocol, devices were recovered by hunters on harvested partridges or from partridge carcasses found on the ground. In the second protocol, grey partridge shooting was suspended, few loggers were recovered by hunters. Recaptures were realized thanks to cages (height 30 * width 40 * depth 30 cm) baited with wheat grain and disposed on the known feeding places and places where sightings of partridges had recently been reported by stakeholders or fieldworkers. When needed, playback calls of territorial males were also used to attract surrounding individuals. All measurements assessed before release were resumed on recaptured birds.

As GPS data inherently contains fixes with erroneous or inaccurate locations, the need to a preliminary screening has been advocated to improve the dataset accuracy (see Bjørneraas, Van Moorter, Rolandsen, & Herfindal, 2010; Lewis, Rachlow, Garton, & Vierling, 2007). Therefore, we applied a filter on our data resulting in a reduction by ca. 4% of the dataset (see Appendix A for details about filtering process).

Statistical analyses

Activity pattern

Activity pattern around the diel cycle was analyzed as distances between successive fixes (see Bengtsson et al., 2014). As interval between fixes was not constant (1 fix / 15min by day *versus* 1 fix / hour at night), data were preliminarily standardized to conserve 1 fix per hour (mean time between successive fixes after cleaning = 60.44 min $\pm$ 1.62 SD). We considered time as time deviation from dawn and dusk times rather than local time, to control seasonal changes in daylight hours induced by large time ranges of the GPS monitoring (from autumn to spring). Time deviations between the time of GPS locations and dawn and dusk times were calculated under the R package *suncalc* (Agafonkin & Thieurmél, 2018). We then modeled the effect of time on activity through generalized additive mixed models (GAMM, negative binomial, log link, cubic regression spline smoothing) under the package *mgcv* (Wood & Wood, 2015), fitted on the distribution of straight-line distances between successive fixes as a function of the time deviation from dawn and dusk. Individual ID was considered as a random factor.

A complementary descriptive analysis was also carried out to investigate whether birds spent all daily activities in the same area or whether variation in movement activity patterns could be related to changes in sites. We assessed the mean distance between the last diurnal and first nocturnal sites at dawn. Fixes were first classified as diurnal (from 75 min after dawn time to 45 min before dusk time), and nocturnal (from 75 min after dusk time to 45 min before dawn time) as periods of homogeneous bird activity according to results of activity pattern (see Results, and Pépin & Fouquet, 1992; Rotella & Ratti, 1988 for activity peaks at dawn and dusk from vocal behaviour). For each individual, each day, the distance was calculated between the centroid of the last grouped-fixes of the diurnal period (at least three successive fixes mutually distant by less than 50 m) and the centroid of the first grouped-fixes of the nocturnal period. Then, a mean distance was calculated by individual. This process was

repeated between the last nocturnal fixes and the first fixes of the next day to assess the mean travelled distance in the morning for each individual.

Habitat selection

GPS data were sectioned in three periods for land cover homogeneity (*autumn*: late-August to mid-November, *winter*: mid-November to mid-March, and *spring*: mid-March to late-May). Compositional analyses rely on analysis of independent individuals (see Aebischer, Robertson, & Kenward, 1993). Because of the gregariousness of grey partridge, we selected within each group of individual (identified through a preliminary screening on Quantum GIS Development Team, 2017), the one that was monitored the longest. Birds monitored less than 7 days were discarded as they remained focused around the release site and prospected area did not reflect habitat availability of the release area. The compositional analysis was only computed on the *autumn* period gathering 22 individuals during daytime, and 13 individuals during nighttime (as in 2015, birds were monitored only during daytime). Too few independent individuals were available for the analysis on wintering and spring periods (5 and 6, respectively). Autumn land-cover was inferred from land-cover surveyed in spring and stored on a GIS database. Five habitat types were used: *harvested crops*, *meadows*, *corn* (main unharvested crop in autumn), *woodlands* and *buildings*.

To investigate whether the habitat selection may vary along the circadian cycle, two compositional analyses (Aebischer et al., 1993) were performed: one on diurnal data and another on nocturnal data. Fixes were classified as diurnal (from 75 min after dawn time to 45 min before dusk time), or nocturnal (from 75 min after dusk time to 45 min before dawn time) according to results of activity pattern analyzes (see Results). Secondly, we determined the proportion of each habitat types available for each individual. The land-cover map was intersected by the Minimum Convex Polygon 100 (MCP100, accounting for 100% of tracking data; Mohr, 1947; White & Garrott, 1990) of each individual, and the proportion of habitats were calculated (see Aebischer et al., 1993). Thirdly, the used proportion of each habitat was determined as the proportion of fixes located in each habitat type (Aebischer et al., 1993). Finally compositional analyses testing for habitat selection hypothesis (nonrandom use of available habitats) were performed as a randomization test with 999 permutations (Aebischer et al., 1993). Habitat were then ranked according to their relative selection. All this process

was realized under the *adehabitat* package (Calenge, 2017) in R software (R Core Team, 2017), supporting the analysis developed in Aebischer et al. (1993).

To test for differences between diurnal and nocturnal patterns of habitat selection, we used paired Wilcoxon-test on the ratio of *habitat use / habitat availability* of each individual monitored during both diurnal and nocturnal periods ($n = 13$).

Nocturnal movements

To investigate factors influencing the probability of grey partridge to undertake nocturnal movements, we first needed to define nocturnal movements. Nocturnal movements were considered as movement of at least 100 m between two clearly identified sites occurring during the nocturnal period (see Appendix B for the calculation details). The frequency of nocturnal movements and the mean distance travelled during these movements were reported.

We tested for effects of distances to predator reservoirs (woodlands, built-up areas) and corridors (hedgerows, roads) on the probability that grey partridge undertook nocturnal movements. First, distance between the centroid of the first roost used at night (defined as at least three successive fixes less than 50 m far from each other, see Appendix B for more details about the first roost identification) and each of the landscape features was assessed. Secondly, for each individual, each night was classified as (1) if the individual undertook nocturnal movement from its first roost, or (0) if not. Then, generalized linear mixed models (GLMM, binomial, logit link) were used to test for effect of distances to each landscape feature (square root transformed) on the occurrence of a nocturnal movement, accounting for individual ID as a random factor. Effect of each variable was assessed by a likelihood ratio-test (i.e. χ^2).

Differences in space use between survivors and non-survivors

We explored differences in space use according to the survival status of birds at 30 days after release (predated, hunted and survivors). Birds were considered as predated when loggers were found on carcass showing predator traces. For each individual, the mean distances to the nearest hedgerow, road/track, woodland and building were calculated for the diurnal (from 75 min after dawn time to 45 min before dusk time), and nocturnal (from 75 min after dusk time to 45 min before dawn time) periods. Effects of survival status, period (diurnal or

nocturnal), and the two-way interaction (survival status x period) were tested through linear mixed-effect models, considering individual ID as random factor. Tukey's multiple comparison tests were performed to contrasts between modality differences with the package *emmeans* (Lenth, Singmann, Love, Buerkner, & Herve, 2019).

We also tested for differences in the mean distance travelled by individuals during nocturnal movements (see the previous section) between groups of the survival status, using linear mixed-effect model with individual ID as random factor.

Lastly, to test whether survival of birds is influenced by their exploration capacity, we compared diffusion coefficient from release to 5 days between individuals with different survival status (predated, hunted and survivors). From fixes recorded within the first 5 days of monitoring (to standardize all individuals independently from their lifespan), we calculated the net-squared displacement (i.e. the squared distance between each fix and release site location). We then modeled the diffusion coefficient as the linear relationship between net-squared displacement and time (Kareiva & Shigesada, 1983; Okubo & Okubo, 1980; Pays et al., 2012), from linear mixed-effect model with individual ID as random factor. To test for differences of diffusion coefficient between groups of survival status, we included the interaction term Time x Survival status in the model. Survival status was only include in the model as interaction term, as we aimed at testing the influence of this variable on the diffusion coefficient, whereas accounting for main effect would have offset the intercept and thus violate the condition that birds diffuse from their release point at time 0 (see Pays et al., 2012 for statistical development).

Results

Activity pattern

Grey partridges activity changed along the circadian cycle. They were less active at night with a mean distance ($\pm$ SD) between successive fixes (1-hour intervals) of 35.0 m ($\pm$ 67.7), than during daytime with 63.0 m ($\pm$ 90.5) (Fig. 1a, b). Grey partridge movement activity peaked from 45 min before to 75 min after dawn and dusk times (Fig. 1a, b). Mean distances travelled between successive fixes during these periods were respectively of 197.5 m ($\pm$ 232.4) and 205.6 m ($\pm$ 229.6) (Fig. 1a, b).

Partridge movements in the evening between the diurnal and nocturnal sites (i.e. for each individual, mean distance between grouped-locations at the end of the diurnal and grouped-locations at the beginning of the nocturnal periods) reached on average 337.40 m ($\pm$ 203.31). Similarly, the mean distance travelled in the morning between the nocturnal and the diurnal sites was 323.86 m ($\pm$ 166.62). These movements were associated with an apparent segregation between diurnal and nocturnal locations (Fig. 1c, d).

Habitat selection

At night, grey partridge exhibited a non-random use of habitats given their availability (Table S2 in Appendix C; randomization test, $n = 13$, $\lambda = 0.145$, $p = 0.016$). Grey partridge preferred, by order of importance, harvested crops > meadows > buildings > woodlands > corn (Table S2). Harvested crops representing short-vegetation covers (stubble fields) or fields free of vegetation (tillage) were more selected than random, and more selected than buildings and woodlands (Table S2), which were avoided (Fig. 1e, grey boxes). Meadows were also more selected than built-up areas at night (Table S2).

During daytime, grey partridge habitat use did not differ to random (Table S3 in Appendix C; randomization test, $n = 22$, $\lambda = 0.514$, $p = 0.524$). However, changes in the ratio of *habitat use / habitat availability* were observed compared to the nocturnal period (Fig. 1e, Table S4 in Appendix C). Grey partridge used fields of harvested crops less (Fig. 1e, Table S4), and used of high-vegetation and refuge covers as corn and woodlands more than at night (Fig. 1e, Table S4).

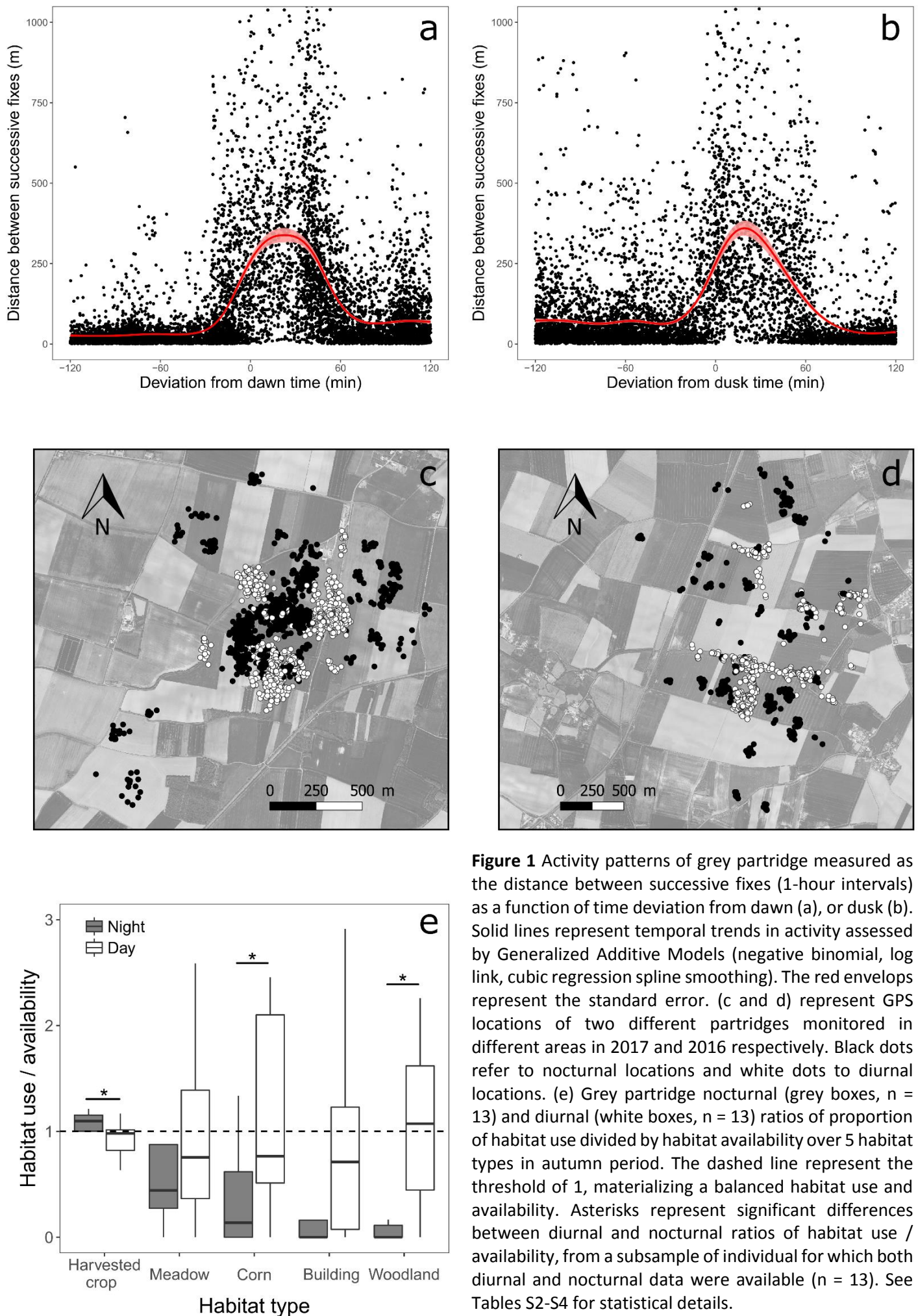


Figure 1 Activity patterns of grey partridge measured as the distance between successive fixes (1-hour intervals) as a function of time deviation from dawn (a), or dusk (b). Solid lines represent temporal trends in activity assessed by Generalized Additive Models (negative binomial, log link, cubic regression spline smoothing). The red envelopes represent the standard error. (c and d) represent GPS locations of two different partridges monitored in different areas in 2017 and 2016 respectively. Black dots refer to nocturnal locations and white dots to diurnal locations. (e) Grey partridge nocturnal (grey boxes, $n = 13$) and diurnal (white boxes, $n = 13$) ratios of proportion of habitat use divided by habitat availability over 5 habitat types in autumn period. The dashed line represent the threshold of 1, materializing a balanced habitat use and availability. Asterisks represent significant differences between diurnal and nocturnal ratios of habitat use / availability, from a subsample of individual for which both diurnal and nocturnal data were available ($n = 13$). See Tables S2-S4 for statistical details.

Nocturnal movements as escape from predator disturbances

First, we observed that 71% of predated partridges for which the time of the death could be estimated (within a precision of 1 hour), were killed at night (10 individuals out of 14).

Nocturnal movements from a roosting site to another, located at more than 100 m, were detected at least once in 84% of birds monitored during night (65 individuals out of 77). Among them, such movements occurred at a mean frequency ($\pm$ SD) of 23.7% (13.0) of the monitored nights, and the mean distance travelled ($\pm$ SD) was 241 m ($\pm$ 82).

The probability that grey partridge undertook these movements was negatively influenced by the distances from the nearest woodland and building, both representing predator reservoirs (Table 2).

Table 2 Effects of the square root transformed distances to woodlands, buildings, hedgerows and roads/tracks on the occurrence (0, 1) of nocturnal movements in grey partridge individuals, tested through generalized linear mixed model (GLMM, binomial, logit link), including individual ID as random factor.

Dependent variable	Independent variables	χ^2 value	df	P value	Estimate $\pm$ SE
Probability to undertake nocturnal movement					(intercept: -0.12 ± 0.35)
	Distance to woodland	8.55	1	<0.01	-0.03 ± 0.01
	Distance to building	4.81	1	0.03	-0.03 ± 0.01
	Distance to hedgerow	0.39	1	0.53	
	Distance to road or track	0.01	1	0.91	

Differences in movement patterns between survivors and non-survivors

Differences in diurnal distance to hedgerows was observed between groups of survival status (Fig. 2a, Table 3a). Hunted partridges were located farther from hedgerows during the day (mean distance $\pm$ SD, 189 ± 163 m) than survivors (81 ± 41 m) and predated partridges (76 ± 73 m) (Fig. 2a, Table 3a). No between-group differences were observed in nocturnal distance to hedgerows (Table S5). Survivor and predated partridges were located farther from hedgerows at night than during the day (respective increases in distances to hedgerows by 73 m and 56 m) while hunted partridges did not (Fig. 2a, Tables 3a and S5).

Differences in distance to roads/tracks were also detected between survival status (Fig. 2b, Table 3b), predated partridges being closer to roads/tracks ($73 \text{ m} \pm 39$) than survivors ($118 \text{ m} \pm 32$) and hunted partridges ($107 \text{ m} \pm 40$) (Fig. 2b, Table 3b). No change in the distance to roads/tracks was found between diurnal and nocturnal periods (Fig. 2b, Table 3b).

Differences in distance to woodlands between diurnal and nocturnal periods were observed regardless of the survival status of birds (Fig. 2c, Table 3c). Finally, no differences in distance to buildings were found (Fig. 2d, Table 3d).

When birds undertook nocturnal movements, differences in distance travelled were observed, hunted birds showing lower distances than survivors (Fig. 2e, Table 3e).

Lastly, analysis testing the effect of the survival status on the strength of the diffusion rate (i.e. relation between net-squared displacement and time) of birds from the release site showed that non-survivor birds (predated or hunted) had a lower diffusion rate from their release during the first 5 days after release than survivors (Fig. 2f, Table 3f).

Table 3 Summary of linear mixed-effect models testing differences in (a) distance to the nearest hedgerow, (b) road/track, (c) woodland, (d) building as a function of the period (*day*, *night*) and of the survival at 30 days after release (*Hunted*, *Predated* or *Survivor*). Modalities taken as reference in tests are in italics. All models include individual ID as random factor. See Table S5 for multiple comparison tests.

Differences in (e) distance travelled during nocturnal movements, and (f) in the strength of diffusion rate (i.e. relation between net-squared displacement and time) from the release site calculated on the first 5 days after release, according to the *survival status* of birds (*hunted*, *predated* or *survivor* at 30 days after release).

Dependent variable	Independent variables	F	df	P value	Estimate ± SE (p)
(a) Distance to hedgerow					(intercept: 81.45 ± 20.90)
	Period	70.82	1	<0.01	
	Survival status	5.22	2	<0.01	
	Period x Survival status	6.18	2	<0.01	Night, Survivor: 73.04 ± 9.26 (<0.01) Day, Hunted: 107.59 ± 30.14 (<0.01) Day, Predated: -5.60 ± 40.20 (0.89) Night, Hunted: -46.76 ± 13.35 (<0.01) Night, Predated: -17.14 ± 17.81 (<0.34) (see Table S5 for multiple comparison)
(b) Distance to road or track					(intercept: 117.84 ± 8.47)
	Period	0.68	1	0.41	
	Survival status	3.81	2	0.03	Hunted: -11.14 ± 12.22 (0.37) Predated: -45.00 ± 16.30 (<0.01)
	Period x Survival status	0.22	2	0.81	
(c) Distance to woodland					(intercept: 117.84 ± 8.47)
	Period	12.34	1	<0.01	Night: 35.40 ± 10.06
	Survival status	0.61	2	0.55	
	Period x Survival status	0.86	2	0.43	
(d) Distance to buildings					
	Period	0.68	1	0.42	
	Survival status	2.77	2	0.07	
	Period x Survival status	0.14	2	0.87	
(e) Nocturnal travelled distance					(intercept: 280.68 ± 15.97)
	Survival status	4.63	2	0.01	Predated: -17.07 ± 33.93 (0.62) Hunted: -94.63 ± 31.16 (<0.01)
(f) Diffusion coefficient					(intercept: 0 ± 0)
	Time	225.41	1	<0.01	
	Time x Survival status	63.88	2	<0.01	Time: 12016 ± 3044 (<0.01) Predated: -3908 ± 6012 (0.51) Survivor: 45151 ± 4371 (<0.01)

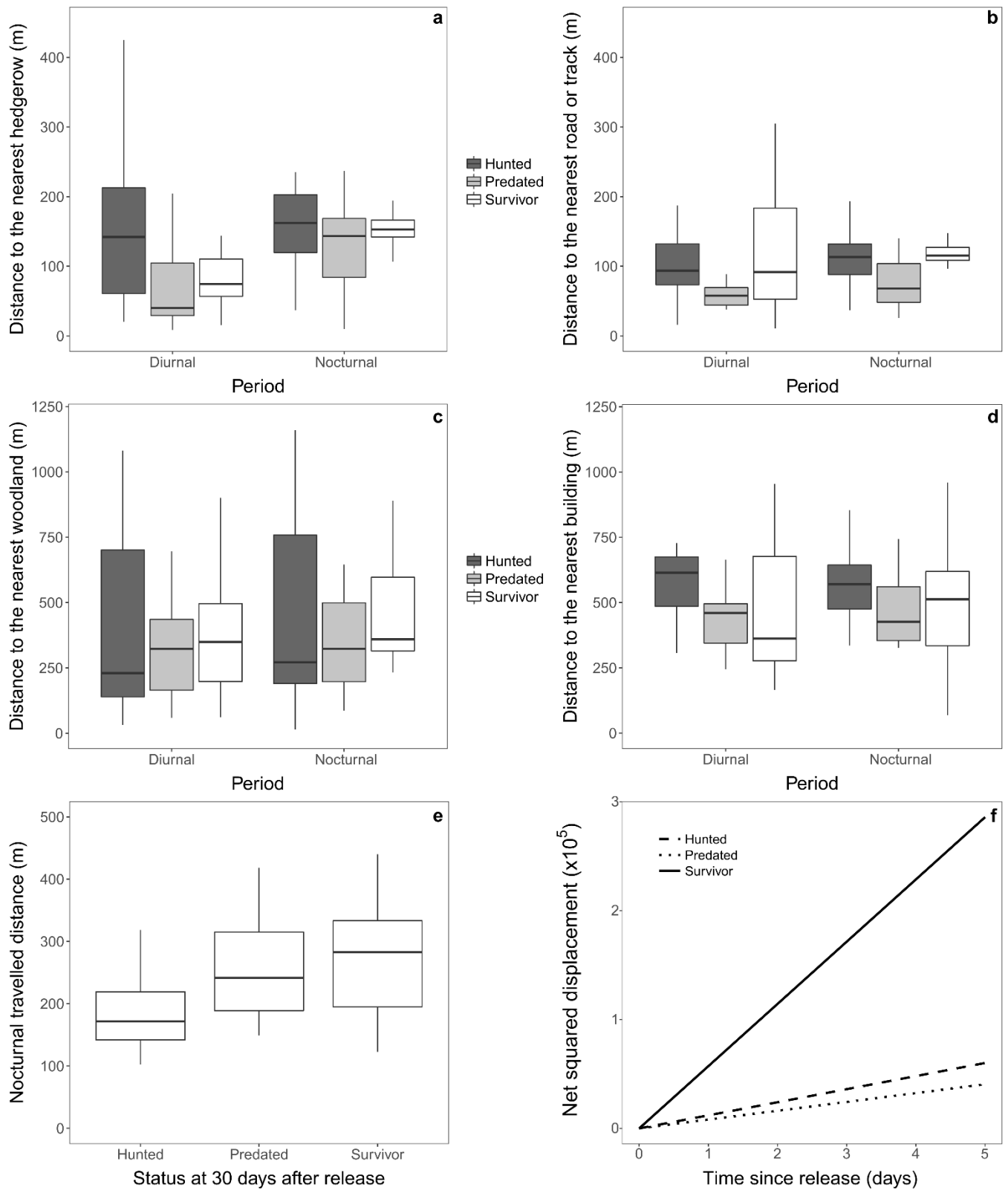


Figure 2 Mean individual distances from the nearest hedgerow (a), road/track (b), woodland (c) or building (d), as a function of the period of the day (diurnal or nocturnal period), and according to the survival status of birds at 30 days after release (Hunted, Predated or Survivor). See Tables 3 and S5 for statistical details. (e) Differences in distance travelled during nocturnal movements (used as a proxy of the escape distance). (f) Diffusion rate (slope between the net-squared displacement and time) from the release site based on the first 5 days after release as a function of the survival status of birds (Hunted, Predated, or Survivor at 30 days after release). See Table 3 for statistical details.

Discussion

This is, to our knowledge, the first study providing GPS monitoring (high temporal resolution with 15-60 min intervals) and individual-based tracking along the diel cycle in grey partridge. Our results showed a variation in activity patterns, space use and habitat selection along the circadian cycle. We found clues suggesting that the behavioural adjustments observed at a population scale, could be shaped by the spatiotemporal structuration of natural (e.g. carnivore predation risk) and human (e.g. hunting activity) disturbances. However, these results were obtained from a released population of captive-reared birds and interpolation to wild populations should be considered with caution.

Grey partridges had greater movement activity at dawn and dusk, which coincides with activity patterns previously described from vocal behaviour (i.e. 45 minutes before the sunrise at dawn and after the sunset at dusk; Pépin & Fouquet, 1992; Rotella & Ratti, 1988). These dawn and dusk movements occurred between diurnal and nocturnal sites, distant by around 330 m. Such changes in space use could be induced by the seeking for different habitat types or structures along the diel cycle (e.g. Tillmann, 2009; Townsend, Rimmer, Brocca, McFarland, & Townsend, 2009). Indeed, at night, partridges avoided high-vegetation covers (corn, the main unharvested crop in autumn), and predator reservoirs (woodlands, buildings ; Dudzinski, 1992; Reitz et al., 2002; Reitz & Mayot, 1999), and preferentially selected short-vegetation covers (harvested crops giving way to stubble or tillage) which could offer a greater visibility for predator detection, and a better ability to escape (Tillmann, 2009; Whittingham, Butler, Quinn, & Cresswell, 2004; Whittingham & Evans, 2004). Conversely, during daylight hours, partridges lowered their use of short-vegetation covers and increased their use of high-vegetation covers (corn, woodlands), which could provide shelters during peaks of human activity as hunting (see Tolon et al., 2009 for the similar behaviour in other game species), and/or against diurnal birds of prey, the second predator group of grey partridge after carnivores (Bro et al., 2013; Tillmann, 2009). However, as grey partridge feeds during daytime (Tillmann, 2009), the diurnal habitat use could also be biased by the location of artificial feeders, commonly used in game management from autumn to spring. Altogether, uses of different sites with different habitat types between day and night by released partridges strongly suggest the existence of a commuting behaviour (see Duriez, Fritz, Said, & Ferrand, 2005). This shift in space and habitat use strategies along the diel cycle could result from an

antipredator behaviour (Duriez et al., 2005; Townsend et al., 2009), allowing a reduction of carnivore predation risk at night and human activity during the day.

Predation death mainly occurred at night (71%), suggesting carnivores as the main predator group, consistently with previous results in France and Western Europe for grey partridge (Bro et al., 2013; Buner & Schaub, 2008; Kamieniarz & Panek, 2011). The higher probability that partridges undertake nocturnal movements when closer to predator reservoirs (woodlands, built-up areas), associated with the high frequency of nocturnal movements (1 night out of 4-5) suggests a high level of nocturnal disturbances caused by predation. This is consistent with Tillmann (2009), reporting nocturnal movements only after an obvious disturbance, and considering distances travelled during nocturnal movements as reliable escape flight distances. These results corroborate the plausible involvement of non-lethal effect of predation in adjustments of space use and habitat selection strategies towards nocturnal avoidance of predator reservoirs (Creel et al., 2005; Townsend et al., 2009).

However, different and inadequate spatial behaviours were also observed in non-survivor birds compared to survivors. Non-survivors were less prone to diffuse from the release site than survivors. Low mobility after release contributes to increase cues of prey presence (e.g. odours in Banks, Norrdahl, & Korpimäki, 2002) thus attracting scent-hunting predators and increasing mortality of low moving animals (Banks et al., 2002). On the other hand, the low diffusion rate of hunted birds could reflect an increased hunting pressure around release sites, where gamebird density is probably higher. Predated birds were closer to roads, used as corridors by carnivores at night (Červinka et al., 2013; Reitz & Mayot, 1999), than survivors. During daytime, hunting activity could act as an alternating pressure. Hunted birds were farther from hedgerows (as potential shelter) and had lower escape distances (distance moved at night as a proxy of escape distance) than survivors, possibly making them more vulnerable to hunting. Overall, inadequate space use patterns could thus induce differences in survival (see also Rantanen et al., 2010 for lower survival associated with proximity to field edges). Direct effects of predation, shooting, thus also contributed to shape the spatial behaviour at a population scale (Lone et al., 2014; Norum et al., 2015), through a counterselection of inadequate behaviours (see also Lone, Loe, Meisingset, Stamnes, & Mysterud, 2015), thus reducing variation in behavioural traits expressed in the population (Homberger et al., 2014).

Changes in individual and population spatial behaviour raise three concerns about the maintenance of populations. First, the counterselection of slow-explorers (i.e. predated and hunted birds with lower diffusion rate from release site) advantage fast-explorers in the short term after release, while they have higher risk-taking behaviours (Sih & Del Giudice, 2012), lower adjustment capacity to changing environments (Quinn & Cresswell, 2005; Verbeek, Drent, & Wiepkema, 1994), and are less likely to persist in the population at medium term (e.g. 12 months later in Hall et al., 2015). Secondly, behavioural adjustments along the diel cycle as a response to disturbances could imply high energetic costs (e.g. escape behaviour by flight, suboptimal quality of habitat used after disturbance; Béchet et al., 2004; Nudds & Bryant, 2000; Tillmann, 2009), impairments in body condition of birds and affect their demography (Béchet et al., 2004; Stillman et al., 2007). Thirdly, in breeding season when pairs are settled and depend on their nesting site, they may face a lower spatial adjustability, while carnivore activity peaks (e.g. in red fox Doncaster & Macdonald, 1997). The high mortality rate of incubating hens caused by predation support this last concern (Bro et al., 2013, 2001).

While releases of partridges and gamebirds before or during hunting season is a thorny subject (inefficient or even counterproductive to maintain population levels in Bro, Mayot, & Mettaye, 2006; alienated form of hunting that raises ethical questions in Sokos, Birtsas, & Tsachalidis, 2008), this study revealed that naïve, captive-reared birds annually released could be shared between natural predators and hunters, and that the few survivors (e.g. 10% in Parish & Sotherton, 2007) could face high costs of behavioural adjustments which could imperil sustainable recovery. Further the case of grey partridge and gamebirds, this emphasize the need to consider natural and human disturbances in agricultural landscapes, along the entire diel cycle, as environmental pressures and potential limits for population recovery, and to minimize them in releasing programs (see also Buner, 2009). Even if observed in few individuals, the spatiotemporal adjustments in behaviour are encouraging and further efforts should focus on how to promote them. First, more consideration should be devoted to increase the antipredator behaviour of released birds, either through parental rather than artificial rearing (Santilli & Bagliacca, 2019), and/or antipredator training before release, improving the ability to cope with predation risk (Beani & Dessì-Fulgheri, 1998; Griffin, Blumstein, & Evans, 2000; Sokos et al., 2008). Secondly, individual traits influence exploratory and antipredator behaviour (e.g. morphology, personality; Lindstrom, Kvist, Piersma, Dekinga,

& Dietz, 2000; López & Martín, 2015). Despite recommendations to account for them in conservation and release programs, individual traits remain disregarded (Berger-Tal & Saltz, 2014; Caro & Sherman, 2012; Mihoub, Le Gouar, & Sarrazin, 2009). Further studies are needed to identify and diversify individual determinants prone to promote behavioural plasticity in antipredator behaviour, ability to escape, and improve the settlement and survival of released populations (Le Gouar, Mihoub, & Sarrazin, 2012; Watters & Meehan, 2007).

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Supporting information

Appendix A. Accuracy assessment and filtering of GPS data

GPS data frequently contains inaccurate and unreliable fixes (Bjørneraas et al., 2010; Lewis et al., 2007). This emphasize the need to assess the precision and then filter out fixes impairing the dataset. Further, Forin-Wiart, Hubert, Sirguy, & Poulle (2015) emphasize the need to test for the accuracy of GPS devices deployed in the present study (CatLog) before deployment on wildlife and proposed erroneous fixes to be identified as location distant from the real position of the GPS device by at least 3-fold the standard deviation of the location error (i.e. the distance between a recorded location and its real position). Therefore, in our study, 77 GPS were tested before deployment. Devices were placed in open area, left static during 2 hours, and programmed to record data every 60 seconds. The location error was evaluated at $16.71 \text{ m} \pm 18.85 \text{ SD}$. However, even if informative about the GPS accuracy, tests in control conditions are limited since no applicable during the monitoring, when real position of animals is unknown. Therefore, the distance between two successive locations is often used as another metric to assess device accuracy. Even though optimally expected to be close to zero (as the GPS was static during the test), this distance was estimated on average at $15.84 \text{ m} \pm 21.49 \text{ SD}$.

Then, divers techniques exist to filter out unreliable locations. A first type of filters is based on index of positioning error given the satellites position (e.g. position dilution of precision) and provided by the GPS devices for each recorded location (Jiang et al., 2008; Langley, 1999; Lewis et al., 2007). Therefore, filters frequently use the number of satellites and/or the dilution of precision to identify unreliable locations (Adrados, Girard, Gendner, & Janeau, 2002; Bjørneraas et al., 2010; Cornélis et al., 2011; Monsarrat et al., 2013). However, the use of such filters is debated as resulting in wildlife tracking datasets to be heavily reduced while large errors remain unfiltered (Bjørneraas et al., 2010). In the present study, such criteria were not convenient as even if location error decrease when increasing the number of satellites available at the recording time (Fig. S1a), most of the most accurate fixes (from a subselection of fixes whose location error was $< 20 \text{ m}$) were recorded when few satellites were available (Fig. S1b). Similarly, high HDOP index usually associated with low accuracy revealed a great accuracy (Fig. S1c), while most of the most accurate fixes (from a subselection of fixes whose location error was $< 20 \text{ m}$) were associated with low HDOP index. Such mismatch

between accuracy index and location error has already been observe in McGregor, Legge, Jones, & Johnson (2014), therefore advocating the use of a second type of filter.

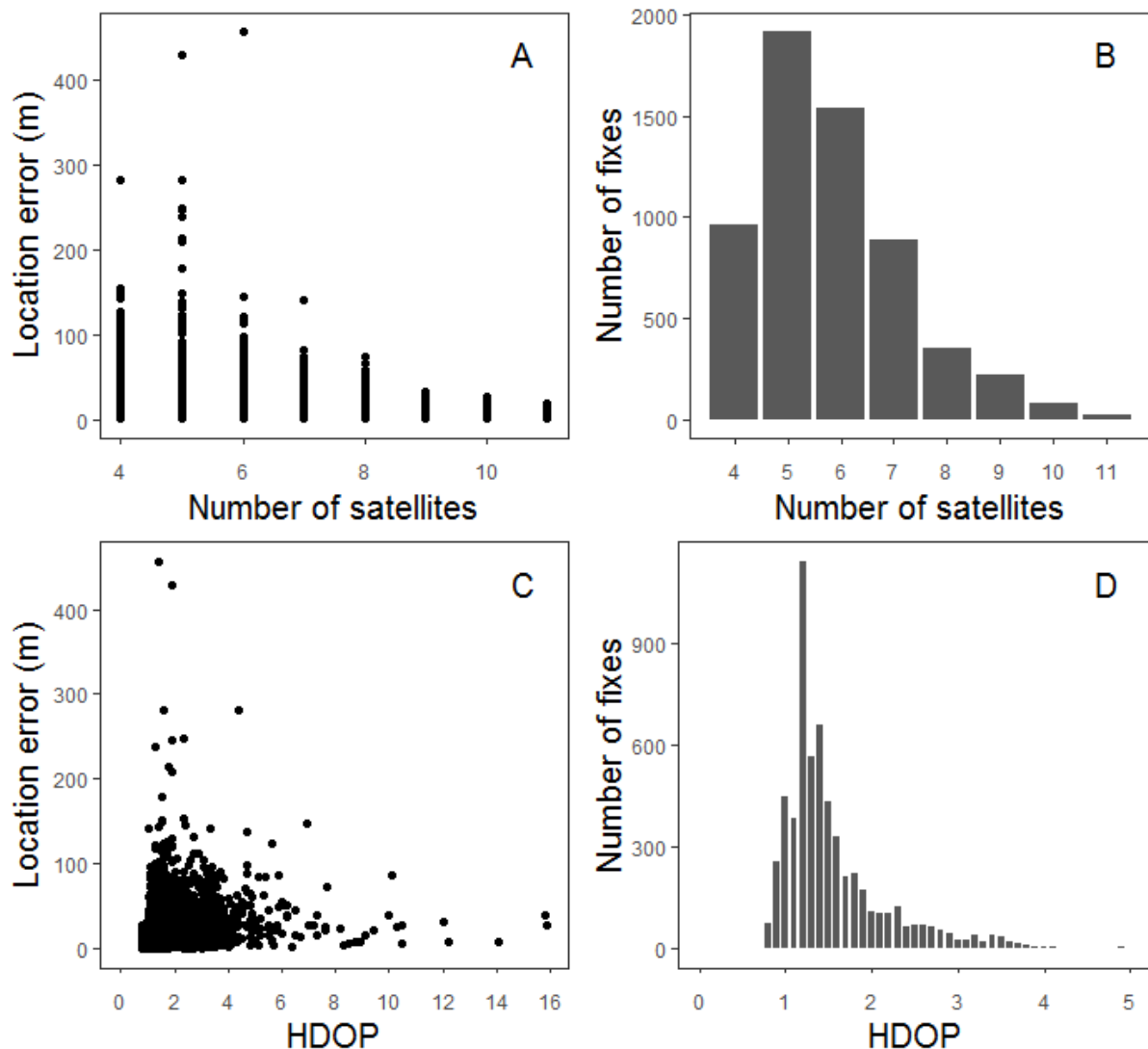


Figure S1 Location error (i.e. distance between the recorded fix and the real position of the GPS device) as a function of the number of satellites at the recording time (A) and of the Horizontal Dilution of Precision (C). Graphs B and D represent the distribution of most precise fixes (subselection of fixes with location error was < 20 m) according to the number of satellites and HDOP index.

A second filter type, based on biology relevance criteria is often used (e.g. Bjørneraas et al., 2010). Such filters aim at identifying implausible movement spikes and discarding erroneous fixes involved. To this end, filters focus on three successive locations, and use different indicators as distances from the previous and to the next fixes, speed, and angle between the three successive locations expressing unreliable round trip (Bjørneraas et al., 2010; McGregor et al., 2014). For instance, in birds, using devices similar to those used in the

present study (CatLog), Kleyheeg et al. (2017) identified erroneous fixes as spikes in movement upper than 100 m and immediately followed by a return by at least halfway in the direction of the original position (with a 15-min interval).

In the present study, we applied simultaneously two filters on three successive locations. For each fix, a first coarse filter was applied. A fix F_t recorded at the time t , is considered erroneous when the turning angle is $> 165^\circ$ and the distance from the last fix and to the next fix are both > 100 m expressing an unreliable round trip. Simultaneously, a second and finer filter is applied, and consider the fix F_t as erroneous when the distance between the previous and the next fixes $d_{F_{t-1}, F_{t+1}}$ is inferior to both distance $d_{F_t, F_{t-1}}$ (between the present fix and the previous one), and the distance $d_{F_t, F_{t+1}}$ (between the present fix and the next one) therefore expressing an unreliable spike movement at the time t . Nevertheless, a minimal condition of 50 m was applied to the distances of $d_{F_t, F_{t-1}}$ and $d_{F_t, F_{t+1}}$ to avoid filtering reliable movements as foraging bouts. After filtering, precision was newly assessed, on controlled conditions and on data recorded *in natura* (Table S1). On controlled conditions, 1.40% of fixes were filtered out and the mean location error varied from $16.71 \text{ m} \pm 18.85 \text{ SD}$ to $15.66 \text{ m} \pm 14.51 \text{ SD}$ (Table S1). The mean distance between two successive locations varied from $15.84 \text{ m} \pm 21.49 \text{ SD}$ to $13.63 \text{ m} \pm 13.19 \text{ SD}$ therefore better controlling to the variance of fix dispersion (Table S1). *In natura*, 4.37% of fixes were filtered out and the mean distance between 2 successive locations varied from $49.57 \text{ m} \pm 96.70 \text{ SD}$ to $41.06 \text{ m} \pm 78.11 \text{ SD}$ (Table S1). This process was replicated on the few other GPS devices, with 0.71% of fixes filtered out bringing the mean distance between two successive locations from $23.87 \pm 80.85 \text{ m}$ to $22.12 \text{ m} \pm 78.15 \text{ SD}$ for UvA-BiTS devices, and 4.19% of fixes filtered out resulting in the mean distance between two successive fixes to be reduced from $45.88 \text{ m} \pm 76.57 \text{ SD}$ to $40.27 \text{ m} \pm 73.95 \text{ SD}$ for Milsar devices.

Table S1 Precision of GPS data assessed before (unfiltered) and after (filtered) filter application on data collected in controlled conditions and *in natura*. The dataset reduction correspond to the proportion of fixes filtered out. The location error correspond to the distance between a fix and the real position of the GPS device at the time of the record (only in controlled conditions). Q95 correspond to the 95% quantiles of distances.

	Controlled conditions		<i>In natura</i>	
	Unfiltered	Filtered	Unfiltered	Filtered
Dataset reduction (%)	0%	1.40%	0%	4.37%
Location error (mean in m $\pm$ SD)	16.71 $\pm$ 18.85	15.66 $\pm$ 14.51	-	-
Q95 of the location error (m)	47.51	42.98	-	-
Distance between two successive locations (mean in m $\pm$ SD)	15.84 $\pm$ 21.49	13.63 $\pm$ 13.19	49.57 $\pm$ 96.70	41.06 $\pm$ 78.11
Q95 of the distance between two successive locations (m)	49.17	39.98	198.65	162.13

Appendix B. Determination of nocturnal movements between different roosts

The discrimination of intrapatch movements (or encamped modes) and interpatch movements (or exploratory modes) has been rather well conceptualized in movement ecology and often rely on turning angles, step length or speed criteria (Barraquand & Benhamou, 2008; Benhamou, 1992; Fryxell et al., 2008). However, this discrimination factors need to be based on highly accurate and high-temporal resolution data. In the present study, the temporal resolution of GPS devices was about a fix per hour at night. As this resolution level did not provide reliable measures of turning angles or speed, we developed a routine to do this, which can be decomposed in three steps. The routine was applied only on nighttime data (from 75 min after the dusk time to 45 min before the dawn time to prevent the inclusion of movement data which peaks around dawn and dusk, see Results).

First, for each night and each individual, we determined the first roosting site as at least three successive locations mutually distant by less than 50 meters (which correspond to the mean distance between successive fixes *in natura*, see Appendix A) far from each other. When a first roost had been identified, the same process was repeated over the 2nd to the 4th fixes in order to check if the next fix was also included in the roost. If fixes were mutually distant by less than 50 meters, the 4th fix was aggregated with the three previous ones. This process was repeated until the condition of mutual distance inferior to 50 meters within the trio of fixes is unsatisfied. The centroid of all locations included in the first roost was calculated.

Then, the second step aimed at identifying a departure from the first roosting site to settle in a second one. The exit was defined as at least two successive fixes located more than 100 meters (2-fold the mean distance observed between successive fixes, see Appendix A) far from the centroid of the first roost, but also mutually distant by less than 50 meters.

This later coupled condition correspond to the third step and simulated the settlement of the bird in a second roost during the night. When these coupled conditions were not satisfied, the last two steps were repeated on the two next fixes until the end of the night. When a second roost was detected, we repeated, as in the first step, the process on the next fixes in order to check and include the next fixes satisfying as well the mutual distance condition. The centroid of the second roost was calculated.

Therefore, a nocturnal change of roosting site was considered solely when all the three present steps were satisfied. Then, the moved distance between both roosts was calculated as the straight line distance between centroids.

Appendix C. Supplementary results

Table S2 Ranking matrix of habitat types on the nocturnal autumnal period (late august to mid-november), based on the proportional habitat use by grey partridge as proportion of fixes of each bird located in each habitat type, compared to the available proportion of each habitat type in the bird's minimum convex polygon (MCP). A triple sign correspond to a significant deviation from random ($p < 0.05$).

	Harvested crop	Meadow	Corn	Building	Woodland	Rank
Harvested crop	0	+	+	+++	+++	4
Meadow	-	0	+	+++	+	3
Corn	-	-	0	-	-	0
Building	---	---	+	0	+	2
Woodland	---	-	+	-	0	1

Table S3 Ranking matrix of habitat types on the diurnal autumnal period (late august to mid-november), based on the proportional habitat use by grey partridge as proportion of fixes of each bird located in each habitat type, compared to the available proportion of each habitat type in the bird's MCP. A triple sign correspond to a significant deviation ($p < 0.05$) from random.

	Harvested crop	Meadow	Corn	Building	Woodland	Rank
Harvested crop	0	+	-	+	+	3
Meadow	-	0	-	+	+	2
Corn	+	+	0	+	+	4
Building	-	-	-	0	+	1
Woodland	-	-	-	-	0	0

Table S4 Results of the paired statistical test assessing changes in the ratio of habitat use / habitat available between nighttime and daytime periods for each habitat type. As data were paired by individual, paired-Wilcoxon-test were used.

Habitat type	Statistic value	P-value
Harvested crop	V = 9	0.008
Meadow	V = 58	0.414
Corn	V = 28	0.022
Building	V = 25	0.363
Woodland	V = 28	0.022

Table S5 Tukey's multicomparison post-hoc tests computed after linear mixed-effect model performed on the grey partridge distance to hedgerows as a function of the interacting effect of the period (day, night) and the survival status of birds 30 days after release (Predated, Hunted, Survivor).

Contrasts	estimate	se	t-ratio	p-value
Day, Survivor – Night, Survivor	-73.04	9.26	-7.89	<0.01
Day, Survivor – Day, Hunted	-107.59	30.14	-3.57	<0.01
Day, Survivor – Night, Hunted	-133.87	30.14	-4.44	<0.01
Day, Survivor – Day, Predated	5.60	40.20	0.14	1.00
Day, Survivor – Night, Predated	-50.30	40.20	-1.25	0.81
Night, Survivor – Day, Hunted	-34.54	30.14	-1.15	0.86
Night, Survivor – Night, Hunted	-60.83	30.14	-2.02	0.34
Night, Survivor – Day, Predated	78.64	40.20	1.96	0.38
Night, Survivor – Night, Predated	22.74	40.20	0.57	0.99
Day, Hunted – Night, Hunted	-26.29	9.62	-2.73	0.08
Day, Hunted – Day, Predated	113.18	40.63	2.79	0.07
Day, Hunted – Night, Predated	57.28	40.63	1.41	0.72
Night, Hunted – Day, Predated	139.47	40.63	3.43	0.01
Night, Hunted – Night, Predated	83.57	40.63	2.06	0.32
Day, Predated – Night, Predated	-55.90	15.22	-3.67	<0.01

Chapitre IV

*Paramètres individuels et ajustements
spatiotemporels aux perturbations : quelles
perspectives pour la gestion?*

Avant-propos et résumé du Chapitre IV

Certaines espèces proies ajustent leur comportement à la variation spatiotemporelle du risque de prédation en se déplaçant vers des habitats moins risqués. Dans le Chapitre III, nous avons mis en évidence que les stratégies individuelles d'utilisation de l'espace et de l'habitat pouvaient influencer sur la survie (prédatés, chassés, survivants à 30 jours après le lâcher). Bien que les individus diffèrent souvent dans leur relation et réponse au risque, et en dépit des recommandations de mieux considérer la variabilité inter-individuelle des traits individuels en gestion des populations, ces déterminants des réponses individuelles restent peu étudiés.

Dans ce chapitre prospectif, nous cherchons à étudier si les traits individuels (personnalité, état sanitaire, biométrie) sont susceptibles d'expliquer les différences interindividuelles observées dans la capacité d'ajustement temporel (au cours du cycle circadien) des oiseaux en termes d'utilisation de l'espace par rapport aux éléments paysagers associés à un fort risque de prédation par les carnivores (haies, routes/chemins, boisements, zones bâties). À partir de recaptures réalisées sur des Perdrix grises en suivi GPS post-lâcher, plusieurs mesures ont été réalisées : des mesures biométriques visant à décrire la condition corporelle des oiseaux, des tests comportementaux visant à déterminer leur personnalité, des analyses immunologiques visant à décrire leur état sanitaire. L'effet de ces traits individuels sur l'ajustement de l'utilisation de l'espace au cours du cycle circadien a ensuite été testé.

Nos résultats montrent que la personnalité et l'état sanitaire (paramètres immunologiques) influent sur la capacité d'ajustement des individus. Les individus les plus téméraires semblent plus en mesure d'ajuster leurs patrons d'utilisation de l'espace, vers un évitement plus important des haies la nuit lorsque l'activité des carnivores est supposée élevée. Les individus en réponse immunitaire forte semblent moins aptes à éviter davantage les éléments paysagers à risque (haies, routes/chemins, boisements) la nuit que le jour.

Une meilleure prise en compte des traits individuels et de leur influence sur les déplacements pourrait permettre d'améliorer le recouvrement et/ou la résilience des populations et gagnerait à être mieux considérée en gestion et conservation des populations. Nous concluons par une discussion sur les implications pour les programmes de recouvrement et de translocation de populations impliquant des individus issus d'élevage, en termes de perte de diversité comportementale et de variabilité immunogénétique comme limites potentielles à la résilience des populations aux pressions environnementales.

**Influence of individual traits on spatiotemporal adjustment to predation risk:
a perspective for management?**

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Abstract

Some prey species are able to adjust their decision-making and behaviour to the spatiotemporal structuration of predation risk, moving towards safer areas and habitats. However, despite individuals often differ in their relation and reaction to the risk, and despite increasing recommendations to consider inter-individual variability in individual traits for management and conservation purpose, such determinants of individual responses have often remained disregarded.

We investigated whether individual traits could influence the behavioural adjustment to risky habitats in grey partridge *Perdix perdix*, an iconic gamebird species in decline since the 1950's, managed through annual releases captive-reared birds. Using a post-release GPS monitoring of captive-reared birds in Central Western France (2016-2018), we examined the relationships between individual traits and the space use behavioural adjustment to risky features (hedgerows, roads / tracks, woodlands, built-up areas) along the diel cycle.

Personality and health status of partridges were linked to patterns of behavioural adjustment to risky features along the diel cycle. Bolder individuals were found to better adjust their space use patterns toward a greater avoidance of hedgerows at night when

carnivore activity is expected to be high. Individuals with a strong immune response exhibited a lower ability to avoid risky features (hedgerows, roads / tracks, woodlands) more at night than during the day.

Synthesis and applications. Space use adjustments of partridges in relation to risky features was influenced by individual traits. Considering such parameters in population management could contribute to improve population resilience or recovery, and should therefore be better considered. We conclude with a discussion on the implications for recovery and translocation programs involving captive-reared individuals in terms of loss of diversity of behavioural traits and immunogenetic variation as potential limits to the resilience of populations to environmental pressures and changing environments.

Key-words

Behavioural adjustment, Captive-reared birds, Grey partridge, Health status, Individual traits, Personality, *Perdix perdix*

Introduction

Predation risk is an ecological process, often spatiotemporally structured (Brown, 1999; Laundré, Hernández, & Altendorf, 2001), whose structuration depends on several factors as the temporal and spatial patterns of predator activity (e.g. Fortin et al., 2005; Lone, Loe, Meisingset, Stamnes, & Mysterud, 2015; Sih, Ziemba, & Harding, 2000), their biased use of habitats (Lone et al., 2015; Norum et al., 2015), and the plurality of predator species (Lone et al., 2014; Norum et al., 2015). To cope with this spatiotemporal variation of risks, some prey species adjust their decision-making and behaviour, to minimize the risk of being predated, moving toward safer areas and habitats (Lone et al., 2015; Tolon et al., 2009). However, in populations, individuals often differ in their response to risky situations (e.g. ability to use high risk habitats, Bonnot et al., 2014; Sih & Del Giudice, 2012). Therefore, despite movements and habitat selection adjustments imply intrinsic individual traits (e.g. individual motivation, ability to move; Nathan, 2008; see also Bonnot et al., 2014; Holtmann, Santos, Lara, & Nakagawa, 2017), individual determinants of the interindividual variability in movements and habitat selection have often been disregarded.

The 'internal state' of animals (i.e. physiological and psychological states, see Nathan et al., 2008) contributes to movement decisions. Animal personality such as boldness influences the risk-taking behavior and affects individual fitness (Both, Dingemanse, Drent, & Tinbergen, 2005; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Sih & Del Giudice, 2012; Smith & Blumstein, 2008). Bolder individuals explore novel environments and return to environments faster after a disturbance (van Oers, de Jong, Drent, & van Noordwijk, 2004; van Oers, Drent, Goede, & Noordwijk, 2004), but could consequently face higher survival costs because of their high risk-taking behaviour (Smith & Blumstein, 2008; van Oers, de Jong, et al., 2004). They also exhibit a lower adjustment capacity to a changing environment (Guillette, Reddon, Hoeschele, & Sturdy, 2011; Quinn & Cresswell, 2005; Sih & Del Giudice, 2012; Verbeek, Drent, & Wiepkema, 1994). Secondly, morphometric traits influence animal 'motion capacity' (*sensu* Nathan et al., 2008). For example, in birds, an increasing body mass or wing load generally impairs the flight abilities as maneuverability (Dietz, Piersma, Hedenström, & Brugge, 2007), take-off velocity and angle (Kullberg, Fransson, & Jakobsson, 1996), and reduce the flight speed (Lindström, Van der Veen, Legault, & Lundström, 2003), therefore impairing the antipredator behaviour (Lindstrom, Kvist, Piersma,

Dekinga, & Dietz, 2000; Lindström et al., 2003). Thirdly, health status interferes with 'navigation capacity' (*sensu* Nathan et al., 2008). Infected individuals demonstrated a reduced locomotion activity because of the energetic costs induced by the immune response (Lindström et al., 2003; Moore, 2002). Therefore, relevant predictors of health status as carotenoid-based coloration and immunity parameters (e.g. leukocyte counts) (Hörak, Ots, Vellau, Spottiswoode, & Møller, 2001; Skarstein & Folstad, 1996; Svobodová et al., 2013; Zuk, Thornhill, Ligon, & Johnson, 1990) are essential to consider as components of movement and habitat selection (Barber & Dingemanse, 2010). Despite numerous and increasing recommendations and warnings about the need to consider inter-individual variability in intrinsic parameters for management and conservation purpose, such traits have often been neglected (Berger-Tal & Saltz, 2014; Caro & Sherman, 2012; Holtmann et al., 2017; Réale, Dingemanse, Kazem, & Wright, 2010; Smith & Blumstein, 2008; Watters & Meehan, 2007).

Grey partridge *Perdix perdix* (Linnaeus 1758), one of the most iconic farmland gamebird in Europe (Aebischer, 1997; Bro, Reitz, & Landry, 2005; Sotherton, Aebischer, & Ewald, 2014), has accused a strong decline for 70 years (Aebischer & Potts, 1994). Remaining populations have now reached so concerning levels in many areas (with even several reports of local extinctions, see Aebischer & Kavanagh, 1997; Chamberlain & Fuller, 2000), that the restoration of self-sustainable populations strongly rely on management through releases of captive-reared birds (Buner, Browne, & Aebischer, 2011). However, captive-reared birds often yield poor survival (e.g. 10% in Parish & Sotherton, 2007), mainly due to vulnerability against predators, because of behavioural deficiencies leading to inadequate use of habitats (e.g. Putaala, Oksa, Rintamaki, & Hissa, 1997; Rantanen, Buner, Riordan, Sotherton, & Macdonald, 2010b, 2010a), morphological and physiological alterations (Putaala & Hissa, 1995). Recently, it has been observed that some individuals were able to adjust their space use behaviour to the spatiotemporal structuration of their environment along the diel cycle (predation risk by carnivores at night, human disturbances during the day) (Harmange et al., *in prep.*). However, despite the recent call for consideration of individual traits in population management, little is known about their influence on the behavioural adjustment to predation risk (but see Homberger et al., 2014), though they may be crucial contributors of the population recovery in agricultural landscapes (fast changing landscapes, high and changing disturbances due to predator risk and human activities).

The present study focused in France, where the grey partridge population has been identified as central to the European conservation of the species (Bro & Crosnier, 2012; Bro et al., 2005), though its maintenance widely depends on releases (Bro & Crosnier, 2012; Reitz, 2003). Released grey partridges may face a high predation pressure at night, and human disturbance during the day (Harmange et al., *in prep.*). From an individual based GPS survey of captive-reared birds, we explored the effect of intrinsic individual parameters (personality, health status, and biometry) on the adjustment of the space use behaviour to risky features along the diel cycle. Risky features were considered as the linear features constituting corridors of carnivore dispersal (hedgerows, roads/tracks Reitz & Mayot, 1999), and predator reservoirs (woodlands, built-up areas ; Dudzinski, 1992; Putaala, Turtola, & Hissa, 2001; Reitz, Le Goff, & Fuzeau, 2002). The behavioural adjustment in space use was considered as the difference between the mean distance an individual is located from each of risky features at the night less the mean distance it is located from these features during the day. This difference can be considered as a proxy of behavioural adjustment against the spatiotemporal structure of disturbances (predator risk at night, human activities during the day). We assumed that the higher the difference, better the individual adjust, avoiding the risky feature at night, and approaching them during the day as refuge or feed-rich habitats. We predicted that bolder individuals would adjust their behaviour better because of their fast exploration capacity, their fast decision-making in front of a risky situation, and their ability to faster return to a place after a disturbance (Table 1). Then, birds in low health conditions were expected to lower adjust their space use behaviour, because of a reduced locomotion activity associated with the high cost of movements (Table 1). Lastly, individuals with a low wing load or body mass were expected to better adjust their space use pattern because of higher flying abilities (Table 1). We also considered two predictions about an effect of the sex on space use adjustments, according to the species biology. First, males could adjust better than females because of their greater mobility and potentially higher flying abilities (see Table 1). Secondly, as a gregarious species (Beani & Dessì-Fulgheri, 1986), no between-sex differences in spatial adjustment could be expected (Table 1).

Table 1 Synthetic table of predicted effects of individual traits on the behavioural adjustment of birds along the diel cycle. Behavioural adjustment is considered as the difference between nocturnal and diurnal distances to features associated with high predation risk (hedgerows, roads / tracks, woodlands, built-up areas). Higher the difference, better the adjustment as higher the avoidance of risky features at night than during the day.

Individual traits	Expected sign of the relationship with behavioural adjustment	Mechanism	References
Personality (boldness)	+	Bolder individual faster explore novel environments, faster return in previously disturbed places	(Sih & Del Giudice, 2012; van Oers, Drent, et al., 2004; Verbeek et al., 1994)
Health status (immune response)	-	Individual in low health conditions (e.g. parasitized) should exhibit a reduced locomotion activity	(Lindström et al., 2003; Moore, 2002)
Wing load	+	Higher the wing load or body mass, lower the flight abilities	(Dietz et al., 2007; Kullberg et al., 1996)
Sex	No difference	Partridges are gregarious and both sex should move in the same group	(Beani & Dessì-Fulgheri, 1986; Bro, 2016)
	Males adjust better	Males are more mobile than females (dispersion, home range) and could be more prone to spatiotemporal adjustments	(Birkan & Serre, 1988; Birkan, Serre, Skibnienski, & Pelard, 1992)

Material & methods

Study site

The monitoring was lead from December 2016 to March 2018 on the Long-Term Socio-Ecological Research site « Zone Atelier Plaine & Val de Sèvre » (LTSER ZAPVS). This area of 435 km² constitute an intensive cereal plain. From 2009 to 2016, land-cover was represented on average by winter cereals (41.5%), sunflower (10.4%), corn (9.6%), rape (8.3%), meadows (13.5%), woodlands (2.9%) and built-up areas (9.8%) (Bretagnolle et al., 2018). The GPS survey was conducted in close collaboration with the Departmental Hunting Federation, and particularly focused on the communal territory of the approved communal hunting society of Marigny, engaged in a 3-year suspension of grey partridge shooting.

For at least 20 years, the density of grey partridge has been very low (Reitz, 2003), and still declining (Harmange, Bretagnolle, Sarasa, & Pays, 2019). In this area where the grey partridge used to naturally occurred, the maintenance of the species is now largely relying on the annual releases of captive-reared birds (Bro & Crosnier, 2012; Reitz, 2003).

Study birds and releasing method

Captive-reared partridges were released by the hunting society in mid-December 2016, mid-September 2017, and late October 2017, following the same protocol: flocks of 12-16 individuals (with a balanced proportion of each sex) released whose 6 to 8 individuals equipped with a GPS device. Birds were left in acclimation pens of ca. 5 m² during 5 days when no trace of predator presence had compelled an early release (after a 3-day acclimation phase otherwise). Apart from this latter case, all birds were released at the same date and no caller individuals were used.

Before being placed into acclimation pens, birds were preliminarily measured (weight, wing length, tarsus length), sexed, ringed (by color and alphanumeric metal gamebird rings), and fitted mainly by data loggers (CatLog-S2, Catnip Technologies Ltd, Hong Kong) on their breast through a necklace. 7 birds were yet fitted by more performing GPS trackers enabling remote data transmission (5 units of UvA-BiTS GPS-trackers, www.uva-bits.nl, Bouten, Baaij, Shamoun-Baranes, & Camphuysen, 2013; and 2 units of Milsar's GsmRadioTag-S9, www.milsar.com). These devices were fitted on their back through a Teflon® harness.

Data collection and preparation for analysis

Loggers were programmed to recorded 1 fix / 15 min during daylight hours and 1 fix / hour at night. This program enabled around 1.5 to 2-month battery lifespan. The remote communication trackers were originally programmed to record 1 fix / 10 min during daylight hours and 1 fix / 30 min at night, and then remotely reschedule to record data at a finer temporal resolution (up to 1 fix / 5 min during daylight hours and 1 fix / 15 min at night) when battery charge allowed.

To download the data recorded from the CatLog devices, equipped partridges had to been recaptured. Recaptures were realized by means of cages (preliminarily protected through top-mounted foam to prevent bird injury), disposed around the release sites, the

known feeding places, and locations where partridges had recently been seen by stakeholders or fieldworkers. Cages were baited with wheat grain, and playback calls of territorial males were additionally displayed when needed to attract surrounding individuals. Capture sites were controlled each 30 minutes. When a bird was caught, the precise location, date and time of the capture were reported. Then, a check-up of the bird was carried out.

First, all measurements assessed before release were resumed (weight, wing and tarsus lengths). Secondly, complementary parameters were collected to evaluate the health status and personality of birds. The health status was determined as the white cell composition, assessed from counting on blood smear (see Hůrak et al., 2001; Skarstein & Folstad, 1996; Svobodová et al., 2013) (see Appendix A for details about the protocol). The red coloration of the carotenoid-based red skin ornaments located behind grey partridge's eye, was analyzed from photographs as another indicator of health status (see Svobodová et al., 2013 and Appendix B for details about the protocol). Thirdly, the personality of birds was assessed through 5 aspects of escape behaviour identified as a measure of bird fearfulness and personality (see Edelaar et al., 2012; Garcia-Longoria, Garamszegi, & Møller, 2014; Møller, Christiansen, & Mousseau, 2011): the *wriggle score*, *feather loss*, *distress call*, *tonic immobility* and *alarm call* (Table S1 in Appendix C for details about behavioural metrics assessment). The flying initiation distance (FID) was also estimated as the distance at which a bird caught in a cage reacted to the straight-line approach of the field operator by a take-off attempt. Approaches towards captured birds were all realized by the same operator, to standardize the approach speed and the operator dress, thus limiting a detectability bias. When all measurements were done, birds were released and the escape flight distance was estimated and reported.

Finally, GPS data recorded on loggers were downloaded. Before analyzing them, we proceeded to a preliminary screening advocated to improve the dataset accuracy by suppressing the inherent erroneous or inaccurate fixes (see Bjørneraas, Van Moorter, Rolandsen, & Herfindal, 2010; Lewis, Rachlow, Garton, & Vierling, 2007). Therefore, data were previously filtered, following the method developed in Harmange et al. (*in prep.*) and resulting in a dataset reduction by around 4%.

Statistical analyses

First, to synthesize the information contained on numerous available metrics of personality on one hand, and health status on the other hand, two Principal Component Analyses (PCA) were carried out. As the major part of birds were recaptured only once (i.e. we had mainly one measure of personality metrics and health status per bird), our data did not permit to account for intra-individual variability. Therefore personality and health status measurements were preliminary averaged by individuals for those recaptured several times. Then, the score of each of the first axis of both PCA were used as a predictor in further analyses.

Secondly, we aimed at determining the effect of biometric parameters, sex, personality and health status on the space use behavioural adjustment of birds. For this analysis, only the 16 recaptured individuals for which all these measurements were available were used. We first calculated for each individual, four metrics of behavioural adjustment as the mean distances of fixes from each risky features (hedgerows, roads / tracks, woodlands, built-up areas) at night (i.e. from 75 min after dusk time to 45 min before dawn time, see Harmange et al., *in prep.*), less the mean distances of fixes from each risky features during the day (i.e. from 75 min after dawn time to 45 min before dusk time, Harmange et al., *in prep.*). The higher the difference, farther the bird from risky features at night than during the day, better the space use behavioural adjustment.

Lastly, linear models were realized considering as dependent variables each of the four differences in distances to risky features along the diel cycle ($\Delta_{\text{nocturnal} - \text{diurnal}}$ distances to risky features). Independent variables used were the sex, a proxy of the *wing load* (i.e. body mass divided by the wing length), the personality (as the first axis of the PCA carried out on personality traits), and the health status (as the first axis of the PCA carried out on immune parameters and coloration of the red skin ornament). Models were selected based on Akaike Information Criterion corrected for small sample size (AICc) (Burnham & Anderson, 2002). Models with a difference in AICc (ΔAICc) of <2 are considered equivalent, and the best model is the minimal model having the lowest AICc value.

Results

The bird's personality was synthesized through a principal component analysis explaining 53.3% of the behavioural variability of individuals on the first two axes dimensions (Fig. 1, see

Table S2 in Appendix C for contributions). High values on the first dimension (PC1) were associated with a high wriggle score, the display of distress calls, a loss of feathers when the bird was held in hand, and a display of alarm calls once released. Conversely, low values were associated with a decrease of previously cited behaviours and with a higher flying initiation distance at the approach of the field operator, a higher flying escape distance when released, and a higher tonic immobility. The first dimension can therefore be used as a proxy of boldness of birds in further analyses: higher the score, higher the individual boldness.

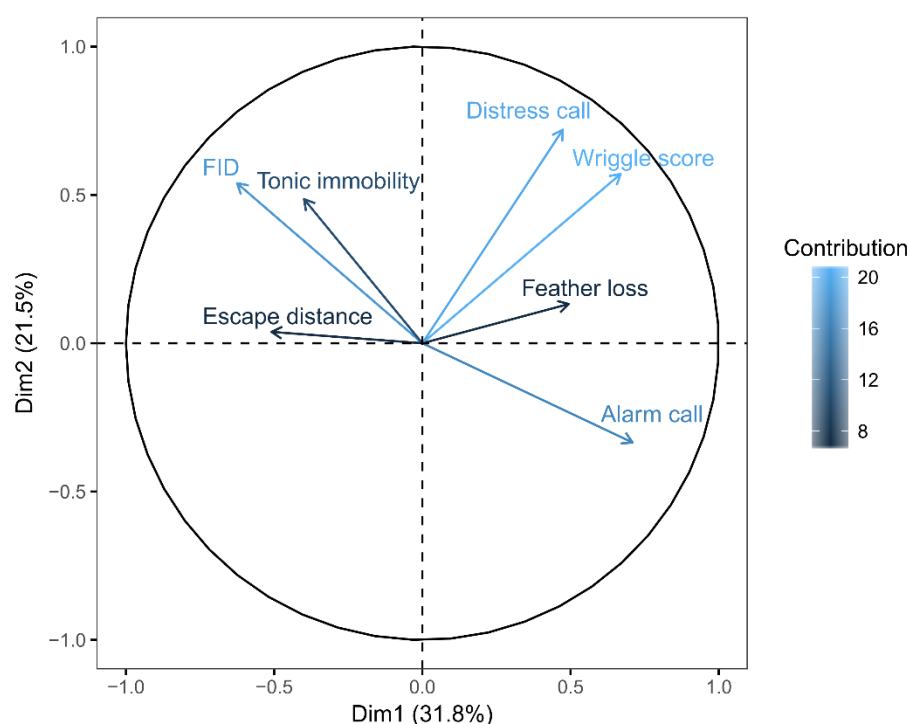


Figure 1 Correlation circle of a principal component analysis synthetizing the information of grey partridge personality. The inertia of each dimension is reported on axes. Details about personality metrics (Table S1) and contributions (Table S2) are available in Appendix C.

The health status of birds was synthetized through a principal component analysis explaining 72.5% of the inter-individual variability on the first two dimensions (Fig. 2, see Table S3 in Appendix C for contributions). High values on the first dimension were associated with a high proportion of leukocytes represented by monocytes and heterophils, the latter being implicated in acute immune responses. Low values were associated with a lower proportion of these leukocytes benefiting to higher lymphocyte and, to a lesser extent, eosinophils proportions.

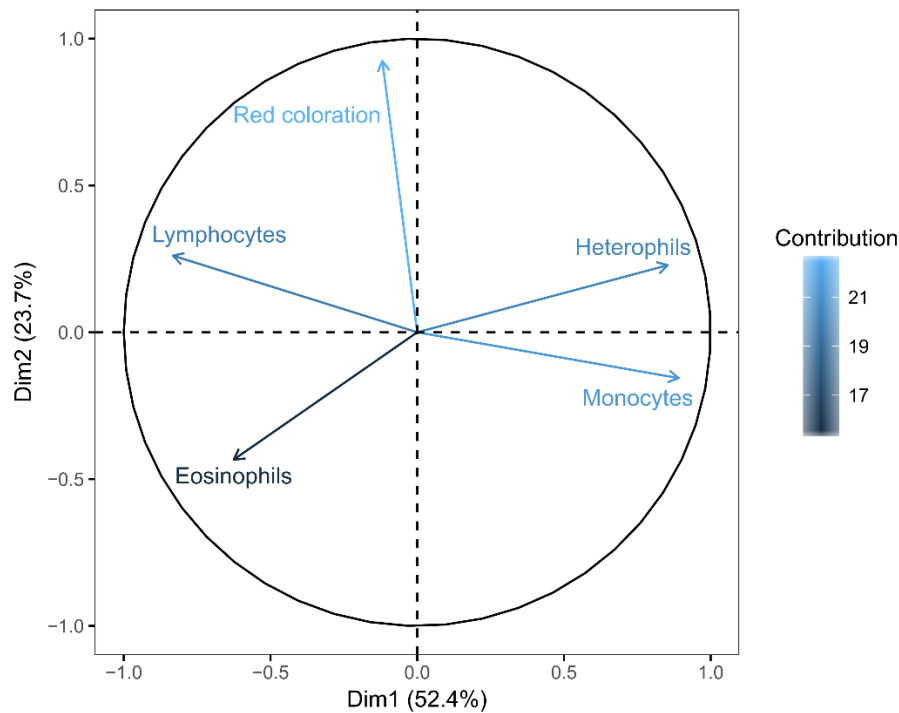


Figure 2 Correlation circle of a principal component analysis synthetizing the health status of partridges from immune parameters. See Table S3 in Appendix C for variable contributions.

Analyses were then carried out to investigate the behavioural adjustment in terms of adjustments in the distances to hedgerows, roads, woodlands and buildings along the diel cycle. The space use behavioural adjustments to hedgerows, roads, woodlands were better explained by the health status of birds (Table 2, see also Table S2 for AICc values of all candidate models). In all cases, the distance to these risky features were negatively related to the first principal component (PC1) of the health status (see Table 3 for estimates). Therefore, higher the score of the health status (PC1), higher the acute immune response by heterophils and monocytes, lower the $\Delta_{\text{nocturnal} - \text{diurnal}}$ distances to risky features, and thus lower the ability of grey partridges to get farther from risky features at night than during the day.

Secondly, the $\Delta_{\text{nocturnal} - \text{diurnal}}$ distances to hedgerows were also positively influenced by the score of the personality PC1 (Table 2, see also Table 3 for estimates). Higher the score of the personality (PC1), bolder the individual behaviour (higher wriggle score, distress call, alarm call, and lower tonic immobility and flight initiation and escape distances), higher the $\Delta_{\text{nocturnal} - \text{diurnal}}$ distances to risky features, and therefore higher the ability of grey partridges to get farther from risky features at night compared to during the day.

No influence of sex and biometric parameters were detected, nor effect of individual traits on the behavioural adjustment in distances to built-up areas along the diel cycle.

Table 2 Summary of AICc and Δ AICc values obtained from models testing the effects of individual traits (health status, personality, sex, biometric parameters) on the behavioural adjustment of space use in relation to risky features (a: hedgerows, b: roads / tracks, c: woodlands, d: built-up areas). Health status and personality correspond to the scores obtained from the first axes (PC1) of the two principal component analyses previously performed. Selected models are represented in bold. Only the top three and null models are shown (see Table S2 in Appendix C for more details, and see Table 3 for estimates).

Dependent variables	Independent variables	AICc	Δ AICc
(a) Δ nocturnal – diurnal distances to hedges	Health status + Personality	149.91	0
	Personality	152.33	2.42
	Health status + Personality + Sex	153.20	3.29
	NULL	158.25	8.34
(b) Δ nocturnal – diurnal distances to roads	Health status	173.71	0
	Health status + Sex	176.60	2.89
	Health status + Personality	176.95	3.24
	NULL	187.45	13.74
(c) Δ nocturnal – diurnal distances to woodlands	Health status	191.98	0
	Health status + Wing load	193.11	1.13
	Health status + Personality	195.05	3.07
	NULL	196.81	4.83
(d) Δ nocturnal – diurnal distances to buildings	Health status	205.31	0
	Health status + Wing load	205.95	0.64
	NULL	206.43	1.12
	Sex	207.86	2.55

Table 3 Estimates of the effects of individual traits on the behavioural adjustment in relation to risky features (a: hedgerows, b: roads / tracks, c: woodlands) from linear models selected in Table 2.

Dependent variable	Independent variables	Estimate ($\pm$ SE)	P value	Adj. R ²
(a) Δ nocturnal – diurnal distances to hedges				0.55
	(intercept)	103.68 (5.42)	<0.01	
	Health status	-7.34 (2.97)	0.03	
	Personality	12.77 (3.81)	<0.01	
(b) Δ nocturnal – diurnal distances to roads				0.63
	(intercept)	18.89 (11.51)	0.12	
	Health status	-34.13 (6.69)	<0.01	
(c) Δ nocturnal – diurnal distances to woodlands				0.34
	(intercept)	103.19 (20.37)	<0.01	
	Health status	-35.41 (11.84)	<0.01	

Discussion

In this study, we first identified behavioural syndromes in birds, as well as immune (or health status) variations in the study population. Our results also revealed an effect of personality traits and immune parameters on the behavioural adjustment in space use patterns, in relation to risky features (predator-rich features or linear features as corridors of carnivores).

A convergence of several personality traits was observed: some individuals were more aggressive or bolder (higher wriggle score, distress call, alarm call) and had a higher risk-taking behaviour (lower flight initiation distances and escape distances), while others were shyer (few or no calls emitted and a low wriggle score when held in hand) and had a lower risk-taking behaviour (higher flight initiation distances and escape distances once released). Shyer individual also exhibit a higher tonic immobility revealing a higher level of fear and stress, than bolder individuals (Edelaar et al., 2012; Møller et al., 2011). This suggest that the first axis of the PCA carried out on personality traits seemed to reliably describe a gradient of boldness in birds. A variation in health status of birds was also observed. Some individuals were characterized by a high proportion of heterophils, monocytes, and a low proportion of lymphocytes. Heterophils are the main granulated leukocytes involved in the acute inflammatory response in Galliforms (Harmon, 1998). Hőrak et al. (2004) also showed an increase in the heterophils counts after a coccidian infection in greenfinches *Chloris chloris* L. 1758. The relative proportion of heterophils to lymphocytes is also used as a proxy of the level of long-term stress in birds (Müller, Jenni-Eiermann, & Jenni, 2011; see also Svobodová et al., 2013 for grey partridge). Increasing proportion of monocytes are mainly provoked by chronic diseases or acute inflammatory responses (e.g. bacteria, parasitism ; Weiss & Wardrop, 2010). Therefore, the high heterophils and monocytes proportions and low lymphocytes proportion identified in the first dimension of the PCA reflect a gradient of acute immune response and level of stress in birds (Weiss & Wardrop, 2010).

The behavioural adjustment of birds in terms of space use to the risky features was influenced by individual traits (health status, personality). Birds under immune responses (high levels of heterophils and monocytes) demonstrated a lower adjustment capacity to three of the four tested risky features (hedgerows, roads / tracks, woodlands) along the diel cycle. They were less able to avoid risky features (associated with carnivore dispersal or concentration) at night than during the day. In grey partridge, the adjustment in space use

patterns along the diel cycle is supposed to occur by commuting flights (Bro, 2016; Tillmann, 2009), between diurnal and nocturnal sites separated by around 300 m (Harmange et al., *in prep.*). Because of the high energetic costs of movements (particularly short flights ; see Nudds & Bryant, 2000), birds in low health conditions could be less able to invest energy in movements due to the costs of struggling against and curing the infection (Lindström et al., 2003; van Dijk et al., 2015). Lindström et al. (2003) showed for example that infected birds had a lower locomotion activity, and take-off velocity after a disturbance than healthy individuals, probably caused by a higher energetic cost and a higher need of energy intake.

Bolder personality is often associated with proactive, more aggressive, fast exploring, and high risk-taking behaviours (Cockrem, 2007; Groothuis & Carere, 2005; Sih & Del Giudice, 2012). Bolder individuals showed a better adjustment capacity to avoid hedgerows more at night than during the day. The pattern of change in avoidance / attraction of hedgerows is expected to be induced by the spatiotemporal structuration of disturbances (predator risk at night and human activities during the day; Harmange et al., *in prep.*). Bolder individuals or high risk-takers could better adjust their behaviour, because of their ability to faster return to an environment after a disturbance than slow-explorers or low risk-takers (van Oers, Drent, et al., 2004). They also tended to develop routines more than slow explorers (Carere, Caramaschi, & Fawcett, 2010), which can explain the greater flexibility around the diel cycle. While such behavioural adjustments could also occur as a response to a disturbance by predator (e.g. increasing probability of nocturnal disturbance near risky features at night in Harmange et al., *in prep.*), bolder individuals may be favoured as they have quick decision-making abilities (Sih & Del Giudice, 2012), compared to shyer individuals which can express inadequate quick decisions as freezing in high predation risk situations (Quinn & Cresswell, 2005). Personality could thus affect the survival of released birds, and bolder individuals or high risk-takers would be better able to cope with multiple pressures on the release site. This is consistent with Harmange et al. (*in prep.*) showing that fast explorers (individuals that have a higher diffusion rate from their release site) had a higher survival 1 month after release than slow explorers, being either predated or hunted.

The effects of both of these individual traits raise question on the long-term maintenance of released populations. After summer releases, grey partridge gather in coveys to overwinter (Beani & Dessi-Fulgheri, 1986). This gregarious behaviour may favour the transmission of

infections (Brittingham & Temple, 1986; Dolnik, Dolnik, & Bairlein, 2010; Moore, 2002), and weaken the adjustment of birds over time. This could also be exacerbated by supplementary feeding through feeders, aggregating birds (Brittingham & Temple, 1986; Höfle, Gortazar, Ortiz, Knispel, & Kaleta, 2004; Millán, 2009). Selecting fast-explorers also raises concerns in highly dynamic agricultural landscape, because of their lesser behavioural plasticity in a changing environment (Quinn & Cresswell, 2005; Sih & Del Giudice, 2012; Verbeek et al., 1994). For example, Verbeek et al. (1994) demonstrated that after a redistribution of food resources, fast explorers would keep going to the former food place, whereas slow-explorers reverse their space use habits more rapidly, and stop going on the former place of food. This could be explained by their lower memory abilities, and the lower accuracy in decision-making (Sih & Del Giudice, 2012). Therefore, selection of bold and fast-exploring individuals could have particularly concerning outcomes on the next breeding period in agricultural landscapes, when habitats are redistributed and the space use adjustment along the diel cycle is not possible anymore, as birds remain near their nest location. Therefore, fast-explorers could be inaccurate in their selection of nesting site according to previous experience of predation risk.

More broadly, several generations of captivity and inbreeding could trigger a loss of genetic and immunogenetic variation (Ewen et al., 2012; Keller, Biebach, Ewing, & Hoeck, 2012). This may also lead to a loss of variation in heritable behaviours such as personality, risk-taking and exploratory behaviours (Dingemanse, Both, Drent, van Oers, & van Noordwijk, 2002; van Oers, de Jong, et al., 2004; van Oers, Drent, et al., 2004; Watters & Meehan, 2007). This loss of genetic variation in captive-reared birds and convergence of behavioural types could consequently impair the behavioural plasticity of birds, their rapid adaptation and the resilience of the released population to changing environments (e.g. predator or competitor introduction, diseases ; Ewen et al., 2012; Keller et al., 2012; Watters & Meehan, 2007). The diversity of behavioural traits and genetic pools in released birds should therefore be considered in releasing programs, to maximize population resilience to environmental pressures and re-establishment success (Ewen et al., 2012; Griffith et al., 1989; Keller et al., 2012; Watters & Meehan, 2007).

However, this chapter as to be considered as a prospective study, and results have to be interpreted with caution. Three limits have been met in this study: First, the influence of individual traits on the behavioural adjustment against risky features was analysed only from

birds which as survived long enough to be recaptured (i.e. more than a month). However, as observed in a previous study (Harmange et al., *in prep.*), a wide variability in space use behaviour was lost during the first month. For example, individuals that diffused slowly from their released sites were more prone to predation and hunting than individuals that diffused faster (Harmange et al., *in prep.*). Therefore, this study is based on a pool of individuals already submitted to selection pressures, and the inter-individual variations studied had already been reduced and were probably not representative of the variation that could be observed in released populations. Secondly, as few recaptures were realized on the same individuals (most of studied birds were recaptured only once), our data did not allowed us to account for intra-individual variability and to test for repeatability in our measurements. Thirdly, as few individuals were available for analysis, we considered all individuals without accounting for the period of monitoring (from winter to spring), which could also have induced a bias in some measurements as coloration, therefore impacting the threshold of allocation of carotenoids in sexual characters or immune response.

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Supporting information

Appendix A. Protocol for the calculation of white cell proportions from grey partridge blood smears

For each recaptured bird, we collected a blood smear to determine the health status of the bird through white cell counts (see Hůrak et al., 2001; Skarstein & Folstad, 1996; Svobodová et al., 2013; Zuk et al., 1990). Birds were placed on their back, a wing spread, and a drop of blood was collected from the brachial vein through a capillary, deposited on a glass slide. Then, another slide was used as spreader, placed at a 45° angle, pushed back towards the blood drop and then pushed across the slide to spread the drop all along.

Back to the lab, blood smears were fixed submerging them during 5-7 minutes in a methanol bath. Then, smears were stained through a Giemsa solution diluted at 1/20. Finally, smear slices were rinsed several times with neutral pH water and left air dry.

The white cell count was carried out with a microscope, under a 1000 × magnification with immersion oil. The number of leukocytes (distinguishing the heterophils, monocytes, lymphocytes, eosinophils, basophils; Campbell & Dein, 1984; Weiss & Wardrop, 2010) counted per a reference number of 10000 erythrocytes were reported. If the total number of leukocytes was lower than 100, the counting was continued until the number of leukocytes counted reached 100, and the supplementary number of each cell type needed to reach this level of leukocyte count were also reported.

Appendix B. Protocol for the colorimetry calculation of carotenoid-based red skin ornaments behind the eye of grey partridge

Each recaptured bird was photographed (Fujifilm FinePix S4000) to assess the coloration of the carotenoid-based red skin ornaments behind its eye, as an indicator of the health status (see Svobodová et al., 2013). Birds were placed outside, without direct sun exposure, in their right-side profile, at a one arm-length distance from the camera lens (approximately 50 cm), and photographed. The same grey standard reference was also placed near birds in each picture (thus in the same exposure and at the same distance from the lens), to standardize coloration measurements between pictures.

Then, pictures were analyzed under the Adobe Photoshop® software, following the method of Lopez-Antia, Ortiz-Santaliestra, Mougeot, & Mateo (2013). An area of 0.20*0.20 cm was selected on the red skin ornament patch. The mean intensity values of Red, Green and Blue (or RGB components) were calculated across all pixels contained within this area (Lopez-Antia et al., 2013). To standardize colour measurements between pictures, these values were corrected using the average RGB values from an area of the same dimension (0.20*0.20 cm) and in the same light exposure conditions on the grey reference (Lopez-Antia et al., 2013).

Lastly, the intensity of the carotenoid-based red skin ornament was calculated as the R value divided by the average of R, G and B values (Lopez-Antia et al., 2013).

Appendix C. Supporting information and results

Table S1 Behavioural metrics assessed as measures of bird personality (see Møller et al., 2011).

Behavioural metric	Assessment	Prediction
Wriggle score	Scored how much a bird struggle when held in a hand: 0 – no movement, 1 – moved rarely, 2 – regularly, 3 – continuously	Individuals that wriggle more should be more likely to escape from a predator when captured (see Møller et al., 2011).
Feather loss	Whether the bird lost feathers (1) during the manipulation, or not (0).	Feather loss can advantage bird caught by a predator, as predator should lose their grip (Møller, Nielsen, & Erritzøe, 2006).
Distress call	Whether the bird gave fear screams (1) when held in hands, or not (0).	Birds displaying fear screams could increase their probability of escape once captured, attracting the attention of secondary predators (Møller & Nielsen, 2010).
Tonic immobility	Before release, the bird was placed on its back on our flat hand and maintained until it was lying still. Then we removed the hand maintaining it and recorded the delay until the bird flew away. The trial was stopped after a delay upper than 30 s.	The longer time a bird stays in the hand, the higher its level of fear (Edelaar et al., 2012; Møller et al., 2011).
Alarm call	Whether the bird displayed alarm call (1) leaving our hand after release, or not (0).	Alarm calls could play a role in the predator distraction to decrease the predation susceptibility of conspecifics, and are expected to be displayed by bolder individuals, placing them in a greater immediate risk (Charnov & Krebs, 1975; Platzen & Magrath, 2004).

Table S2 Variable contributions from the principal component analysis carried out on personality traits (see Fig. 1).

Variable	Dimension 1	Dimension 2	Dimension 3	Dimension 4	Dimension 5
FID	17.546	19.385	1.831	8.153	10.106
Wriggle score	20.084	21.688	1.938	3.235	0.487
Feather loss	10.939	1.162	47.862	0.007	14.257
Distress call	10.084	34.494	0.199	12.352	5.180
Tonic immobility	7.153	15.715	0.004	68.102	0.124
Escape distance	11.615	0.097	48.165	0.001	16.633
Alarm call	22.579	7.458	0.000	8.150	53.213

Table S3 Variable contributions from the principal component analysis carried out on health status (immune parameters, see Fig. 2).

Variable	Dimension 1	Dimension 2	Dimension 3	Dimension 4	Dimension 5
Red coloration	0.538	71.972	9.086	18.401	0.003
Heterophils	27.821	4.399	13.843	35.032	18.905
Eosinophils	14.914	15.834	43.087	6.439	19.727
Monocytes	30.301	2.055	9.880	35.065	22.699
Lymphocytes	26.427	5.740	24.103	5.064	38.666

Table S4 AICc and Δ AICc values obtained from all models testing the effects of individual traits (health status, personality, sex, wing load) on the behavioural adjustment of space use in relation to risky features (a: hedgerows, b: roads / tracks, c: woodlands, d: built-up areas). Health status and personality variables correspond to the scores obtained from the first axes (PC1) of the two principal component analyses previously performed respectively on immune parameters and behaviours. Wing load correspond to the body mass of birds divided by their wing length. Models were ranked by decreasing importance of AICc values.

Dependent variables	Independent variables	AICc	Δ AICc
(a) Δ nocturnal – diurnal distances to hedges	Health status + Personality	149.91	0
	Personality	152.33	2.42
	Health status + Personality + Sex	153.20	3.29
	Personality + Sex	153.55	3.64
	Health status + Personality + Wing load	153.86	3.95
	Personality + Wing load	155.26	5.35
	Health status	156.13	6.22
	Personality + Sex + Wing load	157.81	7.90
	NULL	158.25	8.34
	Health status + Personality + Sex + Wing load	158.48	8.57
	Health status + Sex	158.59	8.68
	Sex	158.61	8.70
	Health status + Wing load	159.50	9.59
	Wing load	161.28	11.37
	Sex + Wing load	161.63	11.72
	Health status + Sex + Wing load	162.16	12.25

(b) Δ nocturnal – diurnal distances to roads

Health status	173.71	0
Health status + Sex	176.60	2.89
Health status + Personality	176.95	3.24
Health status + Wing load	177.35	3.64
Health status + Personality + Sex	180.37	6.66
Health status + Sex + Wing load	180.93	7.22
Health status + Personality + Wing load	181.29	7.58
Health status + Personality + Sex + Wing load	185.39	11.68
NULL	187.45	13.74
Personality	189.73	16.02
Sex	190.10	16.39
Wing load	190.42	16.71
Personality + Wing load	192.95	19.24
Personality + Sex	193.10	19.39
Sex + Wing load	193.72	20.01
Personality + Sex + Wing load	197.23	23.52

(c) Δ nocturnal – diurnal distances to woodlands

Health status	191.98	0
Health status + Wing load	193.11	1.13
Health status + Personality	195.05	3.07
Health status + Sex	195.60	3.62
NULL	196.81	4.83
Health status + Sex + Wing load	197.36	5.38
Health status + Personality + Wing load	197.40	5.42
Personality	198.91	6.93
Wing load	199.02	7.04
Sex	199.29	7.31
Health status + Personality + Sex	199.36	7.38
Sex + Wing load	201.36	9.38
Personality + Wing load	202.09	10.11
Personality + Sex	202.15	10.17
Health status + Personality + Wing load	202.66	10.68
Personality + Sex + Wing load	205.51	13.53

(d) Δ nocturnal – diurnal distances to buildings

Health status	205.31	0
Health status + Wing load	205.95	0.64
NULL	206.43	1.12
Sex	207.86	2.55
Wing load	207.90	2.59
Sex + Wing load	208.00	2.69
Health status + Personality	208.40	3.09
Health status + Sex + Wing load	208.42	3.11
Health status + Sex	208.44	3.13
Personality	208.59	3.28
Health status + Personality + Wing load	210.27	4.96
Personality + Sex	210.89	5.58

Personality + Wing load	211.14	5.83
Personality + Sex + Wing load	212.35	7.04
Health status + Personality + Sex	212.37	7.06
Health status + Personality + Wing load	213.74	8.43

Discussion générale

L'étude du processus de sélection de l'habitat et plus généralement des déplacements d'un animal dans son environnement nous informe sur les pressions auxquelles il est soumis (disponibilité de la ressource, compétiteurs, prédateurs, *etc.*). L'étude des mécanismes sous-jacents (réponses comportementales) des populations aux variations de leur environnement est essentielle pour identifier de potentiels facteurs limitant ces populations. L'objectif de cette thèse était d'étudier l'effet de la dynamique de l'habitat, de la compétition interspécifique et des perturbations naturelles et anthropiques sur les populations de Perdrix grise (via une analyse du processus de sélection de l'habitat et des déplacements, notamment grâce à l'apport de la technologie GPS chez l'espèce Perdrix grise), ainsi que l'influence des traits individuels sur l'ajustement comportemental. Ces questionnements ont été abordés dans un contexte de population de faible densité, soumise à gestion cynégétique mixte (apports annuels d'oiseaux d'élevage, sans arrêt de la chasse).

La dynamique temporelle (1997 – 2017) des patrons de sélection de l'habitat a été étudiée au niveau populationnel, au moyen de modèles de distribution d'espèce (Chapitre I, données diurnes en période de reproduction mises en relation avec des métriques paysagères). L'effet de la compétition interspécifique sur l'accès à l'habitat a été étudié par une analyse des comportements territoriaux des Perdrix grise et rouge (points d'écoute avec repasse audio), et les conséquences sur l'accès à l'habitat ont été analysées par modélisation de niche (Chapitre II). À partir de suivis individuels par GPS (individus d'élevage en phase post-lâcher, Chapitres III & IV), les variations de rythme d'activité de déplacement, de sélection de l'habitat et d'utilisation de l'espace au cours du cycle circadien ont été quantifiées, afin d'évaluer les réponses individuelles aux variations spatiotemporelles des perturbations naturelles (risque de prédation) et anthropiques (activité cynégétique), et l'impact sur leur survie (Chapitre III). L'influence des traits individuels (personnalité, état sanitaire, biométrie) sur l'ajustement comportemental a également été examinée (Chapitre IV).

Dans un paysage agricole influencé par l'intensification des pratiques (entre 1997 et 2017 : +20% de densité de céréales, augmentation de la taille des patches de cultures de 4.7 à 6.3 ha, diminution de la diversité des cultures ; Chapitre I), des changements de sélection de l'habitat ont été mis en évidence au niveau populationnel en un temps relativement court (21 ans). La surface des patches d'habitats favorables a diminué de 26%, et la densité d'observations de Perdrix grise a également chuté (Chapitre I). Un évitement des éléments

paysagers associés à un fort risque de prédation par les carnivores a été observé (par exemple les individus sont localisés 19.5% plus proches des boisements aujourd'hui qu'en 1997–2001 ; Chapitre I, à partir de données diurnes en saison de reproduction). Les suivis GPS réalisés en phase post-lâcher (automne) confirment cette utilisation diurne des boisements (Chapitre III).

Dans ce même paysage, nos résultats suggèrent une compétition interspécifique asymétrique entre les Perdrix grise et rouge (Chapitre II). L'intensité du comportement territorial de la Perdrix grise diminue et un déplacement de niche dans le sens opposé au cœur de niche de la Perdrix rouge est observé en situation de co-occurrence des deux espèces alors qu'aucun changement (comportement territorial, niche) n'est observé pour la Perdrix rouge (Chapitre II, saison de reproduction).

Les suivis individuels par GPS, nous ont permis de mettre en évidence des changements de rythmes d'activité, de sélection de l'habitat et d'utilisation de l'espace au cours du cycle circadien qui suggèrent une réponse comportementale à la variation des perturbations environnementales. La Perdrix grise préférerait des milieux ouverts la nuit (champs à végétation rase, évitement des habitats réservoirs de prédateurs), et des milieux fermés la journée (utilisation plus importante des boisements et champs de maïs, et moins importante des champs à végétation rase). Les pics de déplacement observés à l'aube et au crépuscule, correspondraient aux déplacements entre des sites aux caractéristiques d'habitat différentes (distants d'environ 330 m). La survie des individus est influencée par leurs patrons de sélection de l'habitat et d'utilisation de l'espace (relations positives entre survie et distance aux routes, distance aux haies la journée, et diffusion à partir du point de lâcher, Chapitre III). Les ajustements comportementaux (variation de la distance aux éléments paysagers associés à un risque élevé de prédation au cours du cycle circadien) sont affectés par les traits individuels (relation positive avec la témérité, négative avec réponse immunitaire ; Chapitre IV).

1. Dynamique de l'habitat et processus de sélection : la qualité de l'habitat peut-elle être limitante ?

Bien que l'intensification de l'agriculture ait été identifiée comme principale cause de déclin des oiseaux vivant en milieux agricoles (Benton et al., 2003; Donald et al., 2001), nos résultats montrent qu'elle se poursuit et affecte la dynamique de l'habitat (Chapitre I). Notre analyse temporelle révèle des changements de sélection de l'habitat au niveau populationnel sur un

temps relativement court (21 ans, voir Chapitre I). L'influence de la disponibilité de l'habitat sur les patrons de sélection était attendue (Brown, 1988; Fretwell & Lucas, 1970; J. Jones, 2001), et jusqu'alors était principalement décrite à partir d'études synchroniques comparant différents contextes paysagers chez la Perdrix grise (sélection des céréales comme habitat de nidification lorsque la proportion des habitats semi-naturels permanents, généralement préférés, est faible ; Panek & Kamieniarz, 2000), ainsi que chez d'autres oiseaux vivant en milieux agricoles (López-Jamar et al., 2011). Notre étude met en lumière le processus d'ajustement temporel de la sélection de l'habitat.

Cependant, l'évitement moins prononcé des éléments paysagers associés à un fort risque de prédation par les carnivores (Chapitre I), suggère un ajustement inadéquat, qui pourrait expliquer le déclin observé (Chapitre I). Ces résultats semblent donc aller à l'encontre d'une sélection optimale de l'habitat, selon laquelle les individus d'une population sélectionneraient les habitats dans lesquels leur chance de succès (reproduction, survie) est la meilleure (Brown, 1988; Fretwell & Lucas, 1970). Sous l'hypothèse de densité-dépendance de la sélection de l'habitat, la diminution observée des densités de Perdrix grise (Chapitre I), aurait également dû participer à accroître la sélectivité des habitats les plus favorables (Fretwell & Lucas, 1970). Chez les oiseaux des milieux agricoles, plusieurs études vont dans le même sens, démontrant un comportement mal adapté (« maladaptive behaviour ») de sélection de l'habitat, affectant le succès reproducteur et/ou la survie (Gilroy et al., 2011; Gilroy & Sutherland, 2007; Morris & Gilroy, 2008; B. A. Robertson et al., 2013; Schlaepfer et al., 2002), et menant parfois à des déclins substantiels des populations (Kokko & Sutherland, 2001; B. A. Robertson et al., 2013).

Le processus de sélection de l'habitat implique des réponses comportementales à des stimuli environnementaux, donc deux types de mécanismes pourraient expliquer ces choix mal adaptés. Le premier repose sur la modification des stimuli environnementaux, telle que la dynamique de l'habitat. La diminution de la qualité et de la disponibilité de l'habitat (perte de 26% de surface en habitats favorables ; Chapitre I) pourrait avoir créé une rupture entre les choix adaptatifs et la qualité actuelle de l'habitat (B. A. Robertson et al., 2013; Schlaepfer et al., 2002). La distribution des couverts végétaux (friches, jachères, chaumes de céréales) et de l'alimentation (graines, insectes) influe sur la distribution des oiseaux vivant en milieux agricoles (Buckingham, Evans, Morris, Orsman, & Yaxley, 1999; Green, 1984b; Henderson, Cooper, Fuller, & Vickery, 2000; Moorcroft et al., 2002; Whittingham et al., 2009). Cependant,

la sélection des habitats associés à une meilleure abondance et diversité alimentaire (adventices, graines, insectes), tels que les bordures de champs (Fried et al., 2009; Green, 1984b; Vickery, Carter, & Fuller, 2002), peut également se retrouver associée à un fort risque de prédation et impacter les dynamiques de populations (Morris & Gilroy, 2008; B. A. Robertson et al., 2013). Green (1984b) montre en effet que les couvées de Perdrix (grise et rouge) préfèrent les habitats offrant une forte densité de nourriture (arthropodes, graines), et que les bordures de champs seraient préférées à ce titre (meilleure abondance de nourriture à 5 m qu'à 50 m de la bordure). Une solution pourrait être d'intervenir sur le compromis coût/bénéfice de l'utilisation des habitats, soit en diminuant le coût associé à leur utilisation (c'est-à-dire en diminuant le risque de prédation, par exemple en contrôlant directement l'abondance des prédateurs, ou en augmentant l'abondance des patches d'habitats favorables dans le paysage pour diminuer la probabilité de rencontre avec un prédateur) et/ou en augmentant le bénéfice tiré de l'utilisation du patch (par exemple en agissant sur le compromis vigilance/alimentation par l'augmentation de la densité de nourriture, favorisant une diminution du temps alloué à la recherche alimentaire et un meilleur investissement dans le comportement anti-prédateur tel que la vigilance). Le projet de démonstration du Game & Wildlife Conservation Trust à Royston (Royaume-Uni) fournit un exemple concret par lequel la recréation d'habitats (habitat de nidification, couverts d'alimentation pour l'élevage des jeunes, couverts hivernaux), la supplémentation alimentaire, et un contrôle de prédateurs a permis de multiplier par 5 les densités de couples reproducteurs de Perdrix grise au printemps entre 2002 et 2010 (Aebischer, 2009; Aebischer & Ewald, 2012; Browne et al., 2009; voir aussi Mérieau & Bro, 2009). Ce succès soutient par ailleurs l'idée d'une qualité de l'habitat limitante dans les milieux agricoles pour le maintien des populations d'oiseaux.

Cependant, un deuxième mécanisme pourrait également expliquer un ajustement mal adapté de la sélection de l'habitat : un changement de composition de la population vers des individus dont les capacités cognitives (capacité à reconnaître un patch d'habitat, perception et/ou réponse au risque) et par conséquent les règles de décisions comportementales individuelles (utiliser un patch d'habitat ou non, quand le quitter) (Brown, 1988), sont altérées. L'augmentation supposée de la proportion d'oiseaux d'élevage au cours du temps dans notre zone d'étude (Chapitre I) aurait pu causer un tel changement comportemental observable au

niveau populationnel. Les individus, nés en infrastructure anthropique (fermes d'élevage) pourraient avoir des préférences d'habitat liées à celles de leur habitat de naissance (zones urbaines, routes), phénomène appelé « induction des préférences par l'habitat natal » (« natal habitat preference induction » ou NHPI ; Davis & Stamps, 2004; Stamps & Swaisgood, 2007). La détection du risque pourrait également être altérée par des déficiences de comportement anti-prédateur (4-5% de temps alloué à la vigilance chez des Perdrix grises d'élevage contre 43% chez des individus sauvages ; Rantanen et al., 2010b; M. Watson, Aebischer, & Cresswell, 2007), affectant en conséquence la perception du risque associée à certains habitats, ainsi que leur sélection (par exemple, sélection des bordures de champs par des Perdrix grises d'élevage responsable d'une mortalité accrue ; Rantanen et al., 2010a).

Notre étude n'a pas permis de dissocier les effets induits par la perte de qualité de l'habitat, des effets liés à l'augmentation supposée d'oiseaux d'élevage dans la population. Cependant, les modifications des patrons de sélection de l'habitat et la diminution des densités d'observation de Perdrix grise, concomitantes avec la perte d'habitats favorables, suggèrent que la capacité d'accueil du milieu a tout de même diminué au cours du temps (voir également Aebischer & Ewald, 2012). Les deux mécanismes discutés, mutuellement non exclusifs, pourraient alors entrer en jeu dans les réponses observées. Toutefois, d'autres mécanismes inexplorés, liés à la gestion mixte des populations, pourraient également contribuer à expliquer des changements de sélection de l'habitat. La sélection de l'habitat peut varier selon l'âge et le sexe des individus (Bairlein, 1983; Sandercock, Martin, & Hannon, 2005; Warnock & Takekawa, 1995). Warnock & Takekawa (1995) mettent par exemple en évidence que les adultes de Bécasseau d'Alaska *Calidris mauri* C. 1857, sont plus sélectifs vis-à-vis de l'habitat que les juvéniles. Dans les populations en gestion mixte, la structure d'âge de la population devrait être altérée par les lâchers annuels massifs d'oiseaux juvéniles (associés aux prélèvements s'exerçant à la fois sur les individus lâchés et les individus sauvages, pouvant mener, à terme, à un remplacement de la population ; Bro, Mayot, et al., 2006; Mauvy et al., 1992; ONCFS, 2014; Ponce-Boutin et al., 2006), et pourrait se traduire par une modification des patrons de sélection de l'habitat au niveau populationnel. Cependant, l'influence de la gestion mixte sur la structuration des populations (âge, sexe), ainsi que les potentielles répercussions sur les dynamiques de populations restent mal connues et gagneraient à être étudiées.

II. *La compétition interspécifique, une contrainte supplémentaire ?*

Dans un paysage agricole dans lequel la disponibilité en habitats favorables a fortement diminué au cours des 20 dernières années (Chapitre I), une altération des interactions interspécifiques (Aebischer & Ewald, 2012; Macdonald, Harmsen, Johnson, & Newman, 2004; Robillard et al., 2013; Weldon & Haddad, 2005), telle que des relations de compétition interspécifiques exacerbées était attendue (Dhondt, 2012; Robillard et al., 2013; Wiens, 1992). Nos résultats suggèrent une compétition interspécifique par interférence entre deux espèces phylogénétiquement et écologiquement proches (Chapitre II). L'existence d'une compétition interspécifique viendrait conforter l'idée qu'une ou plusieurs ressources, convoitées par les deux espèces sont limitantes, condition nécessaire à la compétition interspécifique (Dhondt, 2012; Wiens, 1992). Les conséquences asymétriques observées sur l'accès à l'habitat (déplacement de niche de la Perdrix grise dans la direction opposée au cœur de niche de la Perdrix rouge *versus* absence de modification de niche de la Perdrix rouge ; Chapitre II), bénéficierait à la Perdrix rouge. La perte d'habitats favorables (Chapitre I), a donc probablement contribué à intensifier la compétition interspécifique (Robillard et al., 2013; Wiens, 1992), ainsi qu'à modeler de patrons de sélection de l'habitat observés au cours des 21 dernières années (Chapitre I). Bien que ce type de compétition ait été très bien étudié en milieux forestiers (P. R. Martin & Martin, 2001b, 2001a), cette étude est, à notre connaissance, la première mettant en lumière une telle relation de compétition chez les oiseaux vivant en milieux agricoles.

L'intensification des relations de compétition interspécifique dans les milieux agricoles pourrait avoir d'importantes répercussions sur les dynamiques de populations d'oiseaux (Dhondt, 2012; P. R. Martin & Martin, 2001b), en raison des coûts substantiels (par exemple en termes de succès reproducteur) induits par la coexistence avec une espèce compétitrice, tels que l'ont montré les expériences d'exclusion d'espèces en compétition pour le site de nidification, menées par P. R. Martin & Martin (2001b, 2001a). L'exclusion de l'espèce dominante engendre un changement de sélection des sites de nidification chez l'espèce dominée vers des habitats plus favorables, favorisant une augmentation du succès reproducteur (de 1,4 à 2,3 juvéniles par nid ; P. R. Martin & Martin, 2001a). Une telle compétition pour le site de nidification serait particulièrement préoccupante pour l'espèce

Perdrix grise, en raison de la capacité de la Perdrix rouge à assurer une double nidification (le mâle et la femelle peuvent chacun couvrir un nid en simultané ; Casas, Mougeot, & Vinuela, 2009; Green, 1984a; comportement également observé chez d'autres espèces du même genre, telles que la Perdrix bartavelle *Alectoris graeca* M. 1804 ; Bernard-Laurent, Anceau, Faivre, Serres, & Tangis, 2017). L'accès aux sites de nidification de qualité pourrait alors être doublement affecté, et les performances de reproduction possiblement supérieures de la Perdrix rouge (productivité supérieure comparé à une nidification simple ; Green, 1984a) la favoriseraient. Notre étude n'a toutefois pas permis de quantifier l'effet de la coexistence avec une espèce compétitrice (et du déplacement de niche associé) sur les paramètres démographiques de la Perdrix grise. La perspective de quantification du succès reproducteur dans les habitats utilisés en situation d'absence ou de co-occurrence avec la Perdrix rouge, gagnerait à être développée.

Au-delà des effets attendus au niveau populationnel, la perte de disponibilité et de qualité des habitats, induite par les changements environnementaux rapides, pourrait avoir d'importantes répercussions au niveau des communautés. Auer & Martin (2013) mettent en évidence une perte des habitats de nidification préférés chez trois espèces de passereaux (Paruline verdâtre, Paruline de Virginia et Paruline à face rouge *Cardellina rubrifrons* G. 1841), qui serait causée par l'effet des changements climatiques sur les interactions plantes-herbivores (intensification de l'herbivorie associée à une diminution de la diversité et de l'abondance des espèces végétales, affectant la composition des sites de nidification ; Brodie Jedediah, Post Eric, Watson Fred, & Berger Joel, 2012; B. A. Roy, Güsewell, & Harte, 2004). Cette modification des habitats a engendré une augmentation du recouvrement entre les caractéristiques d'habitat des sites de nidification sélectionnés par ces trois espèces. Une diminution du succès reproducteur sur le long terme, causée par l'augmentation des taux quotidiens de prédation des nids a été observée en conséquence (Auer & Martin, 2013). Ces auteurs soulignent que ces changements d'habitats médiés par les changements climatiques pourraient avoir des effets démographiques substantiels chez d'autres espèces au sein de la communauté. Si de tels effets sont causés par les changements climatiques, qu'en est-il de l'impact des changements rapides d'habitats induits par la dynamique d'occupation du sol dans les milieux agricoles ? L'influence de ces changements d'habitats sur les interactions interspécifiques gagnerait à être davantage considérée comme potentiel facteur additionnel

affectant les dynamiques de populations, et les communautés d'oiseaux vivant en milieux agricoles intensifs (voir aussi Newton, 2004).

L'apport d'espèces non-natives pourrait également constituer un facteur aggravant, contribuant à augmenter les surfaces de contact entre espèces phylogénétiquement et écologiquement proches, et favorisant en conséquence une intensification des relations de compétition pour une ressource limitante (Bicknell et al., 2010; Carpio et al., 2017; Laikre, Palmé, Josefsson, Utter, & Ryman, 2006; Renzoni, 1974; P. A. Robertson, 1996). Le déplacement de niche observé chez la Perdrix grise en situation de co-occurrence avec la Perdrix rouge (Chapitre II), vérifie les prédictions de Hardin (1960) (différenciation écologique suite à la remise en contact d'espèces biogéographiquement séparées), et pourrait potentiellement s'accompagner de coûts liés à la coexistence (P. R. Martin & Martin, 2001b). Les introductions d'espèces non-natives phylogénétiquement proches, communément réalisées dans un but cynégétique (Carpio et al., 2017; Jeschke & Strayer, 2006; Laikre et al., 2006; Musil & Connelly, 2009; P. A. Robertson, 1996), posent alors question dans le sens où elles s'affranchissent des questionnements évolutifs, passant outre le passé évolutif des espèces (par exemple la parapatrie compétitive entre Perdrix grise et rouge suggérée par leurs distributions originelles peu chevauchantes et leurs exigences écologiques proches ; Bull, 1991; Cramp & Simmons, 1980; G. E. Watson, 1962). Par ailleurs, d'autres effets en cascade sur les interactions trophiques avaient déjà été mis en évidence. Par exemple, les lâchers de Faisan de Colchide modifient la composition chimique et végétale du sol dans les cages de pré-lâcher (augmentation du phosphate et du potassium, du sol à nu, diminution de la diversité spécifique végétale ; Sage, Ludolf, & Robertson, 2005), ainsi que des habitats environnants (dans les haies alentours, augmentation du sol à nu, diminution des espèces végétales pérennes, des plantules d'arbres et d'arbustes ; Sage, Woodburn, Draycott, Hoodless, & Clarke, 2009). La composition d'insectes dans les bois gérés pour le Faisan est également modifiée (modification de la composition en *Carabidae* ; Neumann, Holloway, Sage, & Hoodless, 2015; diminution de la biomasse de chenilles ; Pressland, 2009), ce qui pourrait affecter la composition des communautés d'oiseaux (Bicknell et al., 2010; Fuller, Noble, Smith, & Vanhinsbergh, 2005). Nos résultats supportent la nécessité de réexaminer cette pratique d'introduction d'espèces non-natives (Bicknell et al., 2010; Sutherland et al., 2006), qui gagnerait à mieux intégrer des considérations écologiques et évolutives.

III. Ajustements aux perturbations naturelles et anthropiques : réponses populationnelles et traits individuels

Le risque de prédation est structuré dans l'espace et dans le temps (Laundré, Hernández, & Altendorf, 2001; Lone et al., 2014; Tolon et al., 2009). Dans les milieux anthropisés, les activités humaines (activités agricoles, activités récréatives) peuvent induire des dérangements, s'additionnant au risque de prédation (Arlettaz et al., 2015; Ciuti et al., 2012; Frid & Dill, 2002; Norum et al., 2015; Zbyryt et al., 2017). Les ajustements comportementaux observés au cours du cycle circadien (rythme d'activité de déplacement, sélection de l'habitat, utilisation de l'espace) chez une espèce proie, la Perdrix grise (Chapitre III), suggèrent une réponse comportementale à la structuration spatiotemporelle du risque de prédation (naturel et anthropique ; Lone et al., 2014; Norum et al., 2015; Tolon et al., 2009). Les changements de sélection de l'habitat observés dans le Chapitre I à partir de données diurnes (évitement moins prononcé des habitats associés à un fort risque de prédation nocturne par les carnivores), pourraient alors être atténués par cette stratégie ou capacité d'ajustement comportemental des patrons de sélection de l'habitat au cours du cycle circadien.

La prédation et la chasse induisent de fortes pressions de sélection, complémentaires et asynchrones, influençant la sélection de l'habitat et les déplacements au sein des populations (Chapitre III) : utilisation en période diurne des seuls couverts refuges disponibles (périphérie des villages, boisements, maïs, haies) et évitement des milieux ouverts (propices aux activités humaines telles que la chasse ; Lone et al., 2014, 2015; Norum et al., 2015) *versus* évitement de ces mêmes habitats refuges en période nocturne (Chapitre III), desquels émergent les prédateurs carnivores, et sélection des milieux ouverts offrant une meilleure détectabilité des prédateurs et une meilleure capacité de fuite (Metcalf, 1984; Tillmann, 2009). Plusieurs études montrent également que l'activité cynégétique s'additionnerait au risque de prédation induit par les prédateurs naturels, multipliant les risques au sein d'un même paysage, et créant un paysage contrasté de risques (voir Lone et al., 2014, 2015; Norum et al., 2015; Tolon et al., 2009). Ces pressions complémentaires et asynchrones façonneraient les patrons spatiotemporels de sélection de l'habitat et d'utilisation de l'espace observés au niveau populationnel, en sélectionnant les individus sur la base de leur comportement de sélection de l'habitat et de déplacement (diffusion à partir du site de lâcher, distances aux habitats associés à un fort risque de prédation), favorisant ceux ayant une capacité d'ajustement

comportemental à la structuration spatiotemporelle des perturbations naturelles et anthropiques (Chapitre III). Lone et al. (2015) mettent également en évidence une sélection par la chasse d'individus de Cerf élaphe *Cervus elaphus* L. 1758 démontrant une plasticité dans leur comportement de sélection de l'habitat. Seuls les individus survivants démontrent un ajustement de leurs préférences d'habitat vers des habitats moins ouverts (visibilité 29% plus courte) après l'ouverture de la chasse (utilisation de zones où le couvert en myrtilles *Vaccinium myrtillus* L. 1753 est réduit de 68%), les autres sont contre-sélectionnés (par prélèvement). Mais quels sont les déterminants individuels de cette capacité d'ajustement comportemental ?

La capacité d'ajustement des patrons de sélection de l'habitat en réponse au risque mobilise des réponses comportementales (Bonnot et al., 2014; Lone et al., 2015), qui devraient être influencées par les traits comportementaux et la relation au risque des individus (téméraires ou timides, enclins ou réticents au risque ; Bonnot et al., 2014; Sih et al., 2012; Sih & Del Giudice, 2012). Jusqu'alors, plusieurs études mettaient en évidence des différences interindividuelles de survie selon l'utilisation de l'espace ou de l'habitat (e.g. les Perdrix grises qui ne survivent pas aux 15 premiers jours suivant le lâcher sont celles qui utilisent le plus les bordures de champs; Rantanen et al., 2010a), mais rares étaient celles ayant exploré les potentiels déterminants de cette variabilité interindividuelle chez la Perdrix grise (voir Homberger, Keller, et al., 2014). Nos résultats suggèrent que les traits comportementaux des individus influencent leur capacité d'ajustement comportemental, ainsi que leur survie (Chapitres III & IV) : les individus qui diffusent rapidement de leur site de lâcher (ou « fast-explorers » *versus* « slow-explorers ») survivent (Chapitre III), et les individus les plus téméraires auraient une meilleure capacité d'ajustement de la sélection de l'habitat au cours du cycle circadien (Chapitre IV). Les individus téméraires, qui explorent rapidement l'environnement (Cockrem, 2007; Sih & Del Giudice, 2012; Verbeek et al., 1994), pourraient être favorisés par leur rapidité de prise de décision et de fuite des prédateurs (Sih & Del Giudice, 2012), ainsi que leur rapidité à réutiliser un habitat après un dérangement (van Oers, Drent, et al., 2004). Les « slow-explorers », plus lents à prendre une décision, restent parfois immobiles en cas de risque élevé de prédation (Quinn & Cresswell, 2005), et seraient quant à eux contre-sélectionnés (Chapitre III). Ces résultats sont en accord avec ceux de Bonnot et al. (2014), montrant que la variabilité interindividuelle des types comportementaux (et du

comportement de prise de risque associé ; Sih & Del Giudice, 2012) influence la capacité des individus à utiliser des habitats selon le risque de prédation/perturbation qui leur est associé, se traduisant en conséquence par des différences interindividuelles de survie. À plus long terme, la contre-sélection des individus « slow-explorers », dont les capacités cognitives seraient supérieures (meilleure mémoire et plasticité comportementale pour inverser un apprentissage antérieur tel qu'une redistribution de la ressource ; Quinn & Cresswell, 2005; Sih & Del Giudice, 2012; Verbeek et al., 1994) pourrait entraîner une perte de capacité d'ajustement des populations aux changements environnementaux rapides tels que la dynamique de l'habitat dans les milieux agricoles (ressource redistribuée plusieurs fois par an). Alors que la sélection du site de nidification est influencée par les types comportementaux (Seltmann, Jaatinen, Steele, & Öst, 2014), cette réduction de la diversité comportementale (et notamment des individus peu téméraires et réticents au risque ou « risk-averse » ; Sih & Del Giudice, 2012) pourrait augmenter la vulnérabilité des populations en période de reproduction, alors que le risque de prédation est maximal (Bro, 2016; Bro et al., 2013; Rymesova et al., 2012), et que l'ajustement spatiotemporel au risque pourrait être réduit, contraint par la localisation fixe du nid à cette période.

Nos résultats montrent également que les individus en réponse immunitaire forte (signe d'une infection) semblent moins aptes à ajuster leur sélection de l'habitat au cours du cycle circadien (Chapitre IV). L'état sanitaire de l'individu pourrait donc également interférer sur la capacité d'ajustement de sélection de l'habitat, par le coût élevé induit par la réponse immunitaire, qui réduirait l'activité locomotrice (Lindström, Van der Veen, Legault, & Lundström, 2003; Moore, 2002), nécessaire à l'ajustement. Ces individus seraient particulièrement vulnérables, à la fois par leur absence (ou déficit) d'ajustement à la variation spatiotemporelle du risque, mais également en raison d'un comportement de fuite altéré par les coûts énergétiques élevés induits par la réponse immunitaire (vitesse d'envol réduite après infection chez le Verdier d'Europe *Chloris chloris* L. 1758 ; Lindström et al., 2003).

Alors que la diversité comportementale conditionne la résilience des populations aux changements anthropiques rapides (Angeloni, Schlaepfer, Lawler, & Crooks, 2008; T. Caro & Sherman, 2012; Cordero-Rivera, 2017; Sih et al., 2012; Watters & Meehan, 2007), et que plusieurs auteurs plaident pour sa meilleure considération en conservation et gestion des populations (voir T. Caro & Sherman, 2012; Cordero-Rivera, 2017), cette étude suggère qu'elle

serait affectée par les pressions de sélection multiples (prédation, chasse), et les perturbations fréquentes associées (fréquence de dérangement nocturne estimée à plus d'une nuit sur cinq dans le Chapitre III, activité cynégétique deux jours par semaine) auxquelles les populations sont exposées. Une réflexion visant à minimiser les pressions afin de conserver la diversité des comportements exprimés dans les populations gagnerait à être engagée (T. Caro & Sherman, 2012; Cordero-Rivera, 2017).

Une considération particulière devrait notamment être portée à l'égard des pratiques de lâcher d'oiseaux d'élevage, qui pourraient également altérer la capacité de réponse des populations renforcées (Smith & Blumstein, 2008; Watters & Meehan, 2007), par la perte de variabilité interindividuelle (génétique, immunogénétique : Ewen et al., 2012; Keller et al., 2012; comportementale : Smith & Blumstein, 2008; Watters & Meehan, 2007), engendrée par la reproduction en captivité à long terme. L'isolement des conditions naturelles, contribuerait également à les rendre naïfs vis-à-vis des menaces de leur futur environnement (pathogènes : Ewen et al., 2012; prédateurs : Griffin, Blumstein, & Evans, 2000; Rantanen et al., 2010b; Sokos et al., 2008). Les capacités d'ajustement et d'adaptation aux changements environnementaux des populations renforcées par ces individus seraient affectées à court terme (vulnérabilité directe des individus lâchés) ou à plus long terme par une altération génétique de la population (hybridation sauvage-élevage ; Duarte & Vargas, 2004; Laikre, Schwartz, Waples, Ryman, & Group, 2010).

Les ajustements spatiotemporels observés en réponse aux fortes perturbations naturelles et anthropiques (dérangements nocturnes fréquents, Chapitre III ; Buner, 2009 relève également que les activités humaines causent deux fois plus de dérangements et de coûts associés que les tentatives de prédation chez la Perdrix grise) soulèvent une question restée en suspens : quels sont les coûts de ces ajustements comportementaux, induits par l'accumulation de ces perturbations ? Pourraient-ils affecter la survie des individus à plus long terme ? Chez l'Oie des neiges *Anser caerulescens* L. 1758, les perturbations induites par les détonations lors de la chasse induisent des distances de fuite plus élevées que les autres perturbations fortuites (par exemple prédateurs naturels ou véhicules), une diminution du gain énergétique après perturbation, et de la condition corporelle des individus dérangés (Béchet, Giroux, & Gauthier, 2004). Cette diminution du gain énergétique serait associée à un repli vers des habitats de moins bonne qualité après la fuite (qualité du patch moindre associé

à un taux d'assimilation réduit ; Béchet et al., 2004), et pourrait être amplifiée par le maintien d'un niveau de vigilance élevé (et la réduction associée de l'alimentation médiée par le compromis vigilance/alimentation ; Riddington, Hassall, Lane, Turner, & Walters, 1996). De telles observations sont également décrites dans les études quantifiant l'impact des activités humaines sur les populations et montrant que les activités humaines induisent des niveaux stress et des coûts énergétiques supérieurs (déplacements, vigilance) à ceux induits par les prédateurs naturels (Arlettaz et al., 2015; Zbyryt et al., 2017). Notre étude n'a pas permis d'explorer la variation intra-individuelle des traits individuels (condition corporelle, état physiologique et immunitaire, comportement) au cours du temps, et son implication sur la capacité d'ajustement comportemental en réponse au risque et sur la survie. Cette question, restée inexplorée dans le cadre de cette thèse, gagnerait à être développée afin de quantifier l'effet à plus long terme de ces perturbations.

IV. Limites et perspectives de recherche

Au cours de cette thèse, nous avons été confrontés à diverses limites, laissant en suspens plusieurs perspectives de recherche qui gagneraient à être développées.

Premièrement, cette étude s'est basée sur une population de Perdrix grise de composition inconnue (proportion d'oiseaux d'élevage), ainsi que sur des suivis GPS d'individus issus d'élevage. Bien qu'une analyse comparative des comportements fins de déplacement (par suivis GPS) avec des individus sauvages fût initialement prévue, ces expérimentations n'ont finalement pas pu être menées en raison de limites d'ordre technique (grippe aviaire notamment). Nos résultats ne nous permettent donc pas de déterminer la part des effets observés (changements de sélection de l'habitat, ajustements comportementaux) qui est expliquée par l'origine des oiseaux. Même s'il y a lieu de penser que des comportements similaires seraient observés dans les populations sauvages (préférences d'habitat analogues à celles décrites pour les populations sauvages, telles que l'importance des céréales comme couvert de nidification : Bro et al., 2013; Bro, Reitz, Clobert, & Mayot, 2000; l'évitement suggéré des villages comme réservoirs de prédateurs : Reitz, Le Goff, & Fuzeau, 2002; l'évitement des boisements comme premier prédicteur de la présence de Perdrix grise à l'échelle communale : Ronnenberg, Strauß, & Siebert, 2016; ou l'ajustement suggéré de la sélection de l'habitat au cours du cycle circadien : Tillmann, 2009), des études

complémentaires gagneraient à être réalisées dans les populations sauvages pour confirmer et approfondir ces résultats (à notre connaissance, aucune étude par suivi GPS fin n'a été réalisée à ce jour dans des populations sauvages de Perdrix grise). Cette limite traduit une lacune plus profonde qui est la méconnaissance de l'influence de l'apport d'oiseaux d'élevage dans le cadre de la gestion cynégétique sur les populations sauvages (le renforcement des populations à but récréatif est moins étudié que le renforcement à but de conservation, voir Champagnon, Elmberg, et al., 2012; voir aussi Bro & Mayot, 2006; Bro, Mayot, et al., 2006; Laikre et al., 2006; Ponce-Boutin et al., 2006). Une question reste donc ouverte : quelle est l'influence des lâchers d'oiseaux d'élevage sur la structure des populations (prévalence d'oiseaux d'élevage, modification de la structure d'âge, modification du sex-ratio) et quelles conséquences (survie, reproduction) pourraient-ils induire ? Alors que les comportements de sélection de l'habitat (Bairlein, 1983; Sandercock et al., 2005; Warnock & Takekawa, 1995), et les taux de mortalité par prédation et par prélèvement (Bro et al., 2013; Calvete, Angulo, & Estrada, 2005; Nadal, Ponz, & Margalida, 2016; Rymesova et al., 2012; Sandercock, Nilsen, Brøseth, & Pedersen, 2011) peuvent être âge- et/ou sexe-dépendants, cette question gagnerait à être étudiée. Notamment, Rymesova et al. (2012) mettent en évidence à partir de l'étude de populations sauvages de Perdrix grise une mortalité différenciée selon l'âge (meilleure survie des individus les plus âgés pendant la période de formation des couples) et le sexe (mortalité supérieure des femelles en période de nidification suggérant un biais du sex-ratio en faveur des mâles) et concluent à une vulnérabilité différente des cohortes face à la prédation. Par ailleurs, en 2016, les oiseaux lâchés par deux des trois ACCA partenaires dans le cadre de notre étude avaient un sex-ratio déséquilibré en faveur des mâles ($sex\ ratio = \frac{n\ mâles}{n\ femelles} = 1,4$ sur l'une et 2,3 sur la seconde ACCA, la troisième avait un sex-ratio de 1). Sur ces mêmes ACCA, le pourcentage de femelles parmi les oiseaux prélevés était respectivement de 53%, 66% et 62% témoignant d'un prélèvement plus élevé sur les femelles (voir aussi Sandercock et al., 2011). Le rajeunissement attendu de la population par l'apport d'oiseaux juvéniles, associé à des lâchers plus important de mâles que de femelles, pourrait affecter la structuration et la dynamique des populations.

Deuxièmement, la diffusion à partir du site de lâcher influence la survie des individus (survie supérieure des oiseaux diffusant plus rapidement ; Chapitre III). Alors que plusieurs pratiques de lâcher visent à sédentariser les oiseaux (pré-lâcher en cage

d'acclimatation, recours à des individus appelants, agrainage sur le site de lâcher, voir Fig. 8a pour un exemple d'individu qui s'établit à 200 m de son site de lâcher et revient régulièrement dessus), la faible diffusion bénéficierait également aux prédateurs (Chapitre III). Comment les techniques de lâcher influencent-elles la diffusion des individus ? Et quelle technique mettre en œuvre pour maximiser la survie post-lâcher ? L'influence des périodes de lâcher, de la nature et de l'âge des oiseaux a été relativement bien étudiée (analyses comparatives de lâchers de compagnies en automne, de couples au printemps, d'adoption de juvéniles au printemps par des couples sauvages en échec de reproduction ; Browne et al., 2009; Buner et al., 2011; Buner & Schaub, 2008). En revanche, les questions relatives à la mise en œuvre opérationnelle des lâchers (par exemple, faut-il lâcher les oiseaux en cage de pré-lâcher « soft release » ou directement « hard release », Bro, 2016) restent peu documentées, débattues et gagneraient à être développées (comm. pers. Elisabeth Bro, 2018). Plus particulièrement, l'influence de l'utilisation de cages de pré-lâcher (qui serait source de blessures, d'exposition aux prédateurs, de stress prolongé et sédentariserait trop les individus ; Bro, 2016; Buner & Aebischer, 2008; mais permettrait une diminution du stress induit par le transport et la manipulation, Jenni et al., 2015) *versus* lâchers directs, de la durée de la phase d'acclimatation (niveau de stress élevé dans les 33 heures suivant la mise en cage d'acclimatation ; Jenni et al., 2015), de la taille des groupes à lâcher, gagneraient à être étudiées. Chez cette espèce grégaire en période hivernale (Beani & Dessì-Fulgheri, 1986), on pourrait s'attendre à ce que lâcher des groupes de grande taille augmente l'inertie de groupe, limite la diffusion (Pays, Fortin, Gassani, & Duchesne, 2012), et expose les populations aux prédateurs. Ces modalités de lâcher sont autant de facteurs cruciaux à considérer, affectant le succès des opérations de translocation des Galliformes (WPA-IUCN, 2009), mais qui restent à ce jour débattues.

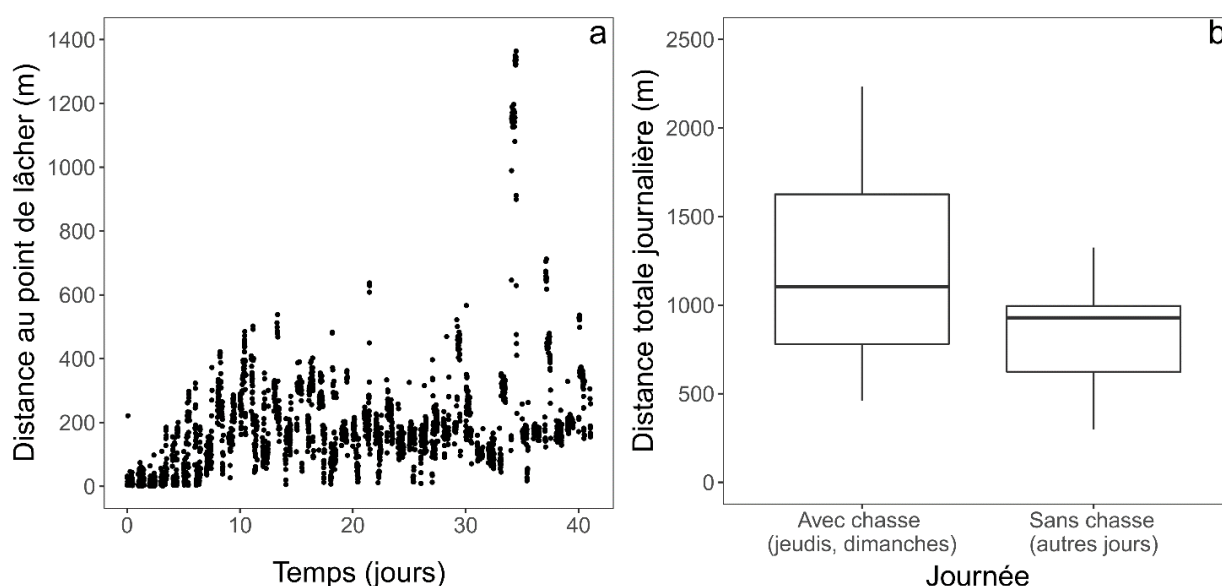


Figure 8 (a) Distance par rapport au point de lâcher en fonction du temps, chez un individu (mâle) de Perdrix grise suivi par GPS en période de chasse 2015 (septembre à octobre) sur la Zone Atelier « Plaine & Val de Sèvre » (Deux-Sèvres, France). On peut notamment remarquer les retours fréquents à proximité du site de lâcher jusqu’au 36^{ème} jour de suivi. (b) distance totale (m) parcourue par jour par ce même individu lors des jours de chasse (jeudis et dimanches) et hors jours de chasse (autres jours).

Troisièmement, au cours de cette thèse, les processus écologiques ont été étudiés à l’échelle interannuelle (Chapitre I, fenêtres glissantes incrémentées par un pas de 1 an), ainsi qu’à l’échelle circadienne (Chapitre III). Mais qu’en est-il de l’échelle infra-annuelle ? Cette question gagnerait à être étudiée étant donné le fort régime de perturbations auquel les individus sont soumis (fréquence de dérangement nocturne estimée à plus d’une nuit sur cinq, activité cynégétique deux jours par semaine), induisant des réponses comportementales (par exemple ajustements spatiotemporels, voir Fig. 8b pour un exemple de déplacements accrus les jours de chasse chez un individu de Perdrix grise sur notre zone d’étude) probablement coûteuses (coûts directs induits par la fuite par le vol, ou indirects via une diminution du temps alloué à l’alimentation ; Béchet et al., 2004; Bélanger & Bédard, 1989; Nudds & Bryant, 2000; voir aussi Arlettaz et al., 2015; Buner, 2009; Zbyryt et al., 2017), qui pourraient affecter leur condition corporelle et menacer leur survie sur le plus long terme (Béchet et al., 2004). Par ailleurs, l’exposition à un risque de prédation élevé pourrait engendrer une diminution de l’investissement dans la fonction immunitaire et rendre les individus plus vulnérables aux pathogènes (voir Navarro, de Lope, Marzal, & Møller, 2004), et altérer en conséquence leur capacité d’ajustement comportemental au risque (Chapitre IV). Ces mécanismes gagneraient

d'autant plus à être étudiés qu'ils permettraient de mieux appréhender les facteurs impliqués dans la décimation progressive des populations entre l'automne (lâchers) et la période de reproduction suivante (seulement 50% des oiseaux lâchés en septembre survivent plus de 3 mois, Mayot et al., 2012; et seulement 10% survivent jusqu'à la saison de reproduction suivante, Parish & Sotherton, 2007). Un suivi individuel « longitudinal » (c'est-à-dire de la variabilité intra-individuelle au cours du temps) de la condition corporelle, des paramètres immunologiques et physiologiques et des comportements spatiaux des individus (déplacements, sélection de l'habitat) permettrait d'étudier et de mieux appréhender les effets induits par les dérangements répétés (risque de prédation, activités humaines) dans les milieux agricoles. Une quantification en parallèle de la variation spatiotemporelle du risque (suivis GPS prédateur-proie, suivi GPS des itinéraires de chasse pour déterminer le paysage de risque induit par cette activité humaine) permettrait d'appréhender la probabilité de rencontre avec un prédateur naturel ou humain et d'étudier plus finement les effets sur les réponses et les paramètres individuels.

V. *Implications pour la gestion des populations de Perdrix grise et d'espèces d'intérêt cynégétique*

La gestion des populations de Perdrix grise nécessite une réflexion globale intégrant un diagnostic du territoire pour identifier les facteurs limitants en matière de paysages, pratiques culturelles, pratiques cynégétiques, et la mise en place de mesures pour les enrayer (Bro, 2016). Cette thèse a permis d'identifier plusieurs limites potentielles au recouvrement des populations de Perdrix grise, et possiblement d'autres espèces d'oiseaux des milieux agricoles : (1) la perte d'habitats favorables induite par l'intensification et la dynamique rapide de l'habitat dans les paysages agricoles, (2) une modification de l'accès à la ressource (habitat) par la compétition interspécifique, potentiellement exacerbée par les lâchers annuels d'espèces phylogénétiquement et écologiquement proches (Perdrix rouge), (3) la présence de fortes pressions de sélection et sources de dérangement naturelles et anthropiques (prédateurs, chasse) pesant sur les populations de faible densité maintenues par des lâchers. Dans les sections précédentes, nous avons pointé différents effets aggravants que pourrait induire la gestion cynégétique mixte des populations de faible densité (lâchers cynégétiques annuels d'oiseaux issus d'élevage, sans arrêt de la chasse).

L'efficacité et le principe même de ce mode de gestion est discuté (inefficace voire même contre-productif pour le recouvrement ou le maintien des populations dans Bro, Mayot, et al., 2006; forme aliénée de chasse qui soulève des questions d'éthique, qui semble apporter plus d'inconvénients que d'avantages, et pourrait contribuer à déconnecter les chasseurs des traditions et de la philosophie de la chasse dans Sokos et al., 2008). Nous défendons l'idée que la gestion par lâcher cynégétique, consistant en des opérations de translocation (au sens général fixé par l'IUCN Species Survival Commission, 2013 ; c'est-à-dire tout déplacement d'individus, qu'ils soient sauvages ou issus d'élevage, et quelle que soit la motivation : conservation, activités récréatives, etc.), gagnerait à s'imprégner des principes de la biologie de la réintroduction, définie comme la science dont l'objectif est d'améliorer l'issue des opérations de translocation (dans Armstrong & Seddon, 2008; voir aussi Ewen, 2012; IUCN Species Survival Commission, 2013; Seddon, 2013).

1. Améliorer la quantité et la qualité des habitats

La dégradation de l'habitat induite par l'intensification de l'agriculture, l'une des principales causes de déclin des populations de Perdrix grise et d'oiseaux vivant en milieux agricoles (Aebischer & Ewald, 2012; Aebischer & Potts, 1994), se poursuit encore aujourd'hui (Chapitre I). Or les opérations de translocation visant à renforcer ou réintroduire des populations sans avoir préalablement remédié aux causes de déclin ne permettent pas la réimplantation de populations viables (Fischer & Lindenmayer, 2000). La qualité de l'habitat est de surcroît identifiée comme la première cause d'échec d'opérations de translocation (le succès d'une opération de translocation correspond à l'établissement d'une population viable ; Griffith, Scott, Carpenter, & Reed, 1989; voir également Fischer & Lindenmayer, 2000; Osborne & Seddon, 2012; Wolf, Griffith, Reed, & Temple, 1996). Madden, Hall, & Whiteside (2018) observent par exemple des mortalités par inanition de Faisans de Colchide lâchés, qui seraient expliquées par la faible capacité d'accueil des milieux (perte de surface en chaumes de céréales et de disponibilité en graines en hiver, arrêt de la supplémentation alimentaire à la fin de la saison de chasse, bien que l'hypothèse de l'incapacité des oiseaux d'élevage à utiliser les ressources alimentaires naturelles ne puisse être écartée ; Mathews, Orros, McLaren, Gelling, & Foster, 2005). Bro (2016) relève également des mortalités par inanition chez la Perdrix grise. La priorité serait donc de rétablir un habitat favorable avant toute translocation

afin de maximiser le succès d'établissement des populations lâchées (IUCN Species Survival Commission, 2013; Osborne & Seddon, 2012; Seddon, 2013).

Ces mesures pourraient de surcroît bénéficier à l'ensemble des oiseaux vivant en milieux agricoles (J. Caro et al., 2015; Estrada et al., 2015; Stoate & Szczur, 2001). Stoate & Szczur (2001) montrent que l'ensemble des mesures de gestion des oiseaux gibiers (gestion de l'habitat, contrôle de prédateurs, alimentation hivernale) favorise une augmentation de l'abondance de passereaux, et plus particulièrement des espèces dont le déclin est concomitant avec l'intensification de l'agriculture (voir aussi Estrada et al., 2015). Sage, Parish, Woodburn, & Thompson (2005) mettent en évidence que les cultures à gibier d'hiver sont utilisées par 26 espèces de passereaux, dont 10 en déclin marqué entre les années 1970 et 2000, et les cultures à gibier d'été abritent 14 espèces de passereaux dont 8 en déclin modéré ou fort et favorisent une densité 7 fois supérieure aux champs cultivés adjacents. Cette attractivité s'expliquerait par la quantité d'arthropodes, d'adventices et de graines qu'elles fournissent (+90% d'espèces d'advantices, 15 fois plus de papillons, 40 fois plus de bourdons, 80 fois plus d'oiseaux que dans les cultures conventionnelles, dans Parish & Sotherton, 2004). L'agrainage en hiver, lorsqu'il est géré de manière appropriée (près de haies, changement de sites régulièrement; Sánchez-García, Buner, & Aebischer, 2015; voir aussi Buner & Sánchez García, 2017 établissant des lignes directrices pour un agrainage bénéfique aux passereaux, minimisant l'utilisation par les espèces non ciblées telles que les corvidés, mustélidés, rongeurs et cervidés), bénéficierait également à de nombreuses espèces d'oiseaux (par exemple à 15 espèces de passereaux, dont 6 à intérêt de conservation au Royaume-Uni dans Sánchez-García et al., 2015; voir aussi Estrada et al., 2015). Ces mesures pourraient également bénéficier à l'ensemble de la biodiversité, comme le soulignent Mustin, Newey, Irvine, Arroyo, & Redpath (2011) qui relèvent plusieurs mesures de gestion initialement développées en faveur des espèces d'oiseaux gibiers, ayant par la suite été intégrées aux mesures agro-environnementales, généralisées pour la conservation de la biodiversité.

2. Repenser les « associations » d'espèces lâchées en considérant la compétition interspécifique

Plusieurs limites à la pratique de lâcher d'espèces non-natives visant à relâcher la pression de chasse sur les espèces natives étaient déjà bien identifiées (favorise par exemple les

prélèvements par inadvertance par tirs ou chiens de chasse sur l'espèce à préserver : Aebischer & Ewald, 2010; observations personnelles sur notre zone d'étude; la compétition indirecte médiée par les parasites : Tompkins, Draycott, et al., 2000; Tompkins, Greenman, et al., 2000; le parasitisme de ponte d'espèces natives : P. A. Robertson, 1996). Cette étude identifie la compétition interspécifique par interférence (Chapitre II), suggérée à plusieurs reprises mais jamais démontrée jusqu'alors (Bro, 2016; Mayot, 2009; Meriggi et al., 1991; Renzoni, 1974), comme potentiel facteur additionnel, limitant le recouvrement des populations de Perdrix grise. Ce facteur serait d'autant plus important à considérer qu'il devrait s'intensifier, alors que la perte d'habitats favorables tend à se poursuivre (Chapitre I), et que les ressources alimentaires tendent à devenir de plus en plus limitantes dans les milieux agricoles (Fried et al., 2009; Robinson & Sutherland, 2002; Sánchez-Bayo & Wyckhuys, 2019).

L'introduction fréquente d'espèces phylogénétiquement proches et non-natives (voir Carpio et al., 2017), interroge d'un point de vue écologique (quels sont les impacts sur la biodiversité des introductions d'espèces réalisées pour soutenir des activités récréatives ? ; Sutherland et al., 2006), d'autant plus que la présence d'espèces proches est par ailleurs bien identifiée comme limite à l'établissement des populations dans le cadre de translocations (52% de succès en présence d'un potentiel compétiteur morphologiquement similaire dans Griffith et al., 1989; voir aussi C. G. Jones & Merton, 2012), et figure parmi les critères de diagnostic pré-lâcher de territoire à évaluer avant translocation en biologie de la réintroduction (IUCN Species Survival Commission, 2013; voir aussi Ewen, 2012). Sa non-prise en compte en gestion cynégétique par le lâcher gagnerait à être reconsidérée, et les « associations » de plusieurs espèces lâchées sur les mêmes territoires, gagneraient à être repensées sur des bases écologiques (Quels impacts sur les interactions interspécifiques ? Sur les réseaux trophiques ?).

3. Réduire les sources de perturbation

La fréquence des perturbations auxquels les oiseaux sont soumis en phase post-lâcher est élevée (déplacements nocturnes en réponse supposée à un dérangement supérieurs à une nuit sur cinq dans le Chapitre III ; en période de chasse, la chasse a lieu deux jours par semaine). La pratique de lâcher d'été avant la saison de chasse et la récolte des cultures de printemps (tournesol, maïs majoritairement), exposent particulièrement les oiseaux à de

fortes perturbations pendant les premières semaines qui suivent le lâcher (activités agricoles, détonations lors de la chasse), et pourraient façonner les comportements spatiaux de la population (par exemple utilisation des boisements et périphérie de zones urbaines le jour dans le Chapitre III, favorisant potentiellement une plus grande probabilité de rencontre avec les prédateurs à la nuit tombée). Alors que Buner (2009) souligne la nécessité de réduire les sources de perturbation (risque de prédation, activités humaines causant deux fois plus de dérangements que les tentatives de prédateurs, avec des coûts énergétiques associés) avant translocation de Perdrix grise, une réflexion visant à minimiser ces sources gagnerait à être développée.

Buner et al. (2011) suggèrent, où les densités de populations sont faibles, de réaliser des lâchers de compagnie à l'automne, en octobre. Une première solution pour limiter le dérangement serait de lâcher les oiseaux en fin de période de chasse. Sur l'ACCA de Marigny (chasse à la Perdrix grise suspendue, mais maintenue pour les autres espèces), nos données montrent un taux de recapture (par cages-pièges mises en place à partir d'un mois après le lâcher) de 11% pour les oiseaux lâchés en septembre 2017, et de 23% pour les lâchers réalisés fin octobre 2017 et mi-décembre 2016. Ces chiffres, donnés à titre indicatif, suggèrent que des lâchers fin-octobre (voire mi-novembre après la clôture de la chasse à la Perdrix), pourraient être envisagés pour limiter le dérangement humain lié à cette activité. Un contrôle de prédateurs avant les lâchers pourrait également limiter le risque de prédation et améliorer la productivité et le recouvrement rapide des populations (voir Aebischer & Ewald, 2012; Buner, 2009). Enfin, les lâchers gagneraient à être systématiquement réalisés en réserves de chasse, dans des habitats de qualité, afin d'exposer les oiseaux au minimum de perturbations anthropiques.

4. Lâcher des oiseaux de qualité

La prédation et la chasse soumettent les populations lâchées à de fortes pressions de sélection (Chapitre III). Ces résultats vont dans le sens des forts taux de mortalité généralement observés lors de renforcements de population à but cynégétique (par exemple, 30 jours après le lâcher, 72 à 95% de mortalité chez la Perdrix bartavelle dans Dessì-Fulgheri, Dondini, Paganin, Vergari, & Beani, 2001; 63% de mortalité chez la Perdrix rouge dans Gortázar, Villafuerte, & Martín, 2000; 81 % de mortalité pour le Faisan de Colchide dans Hessler, Tester,

Siniff, & Nelson, 1970; 73 à 90% de mortalité chez la Perdrix grise dans Rymesova et al., 2013), impliquant majoritairement la prédation (par exemple 60 à 80% des mortalités observées chez la Perdrix grise dans Bro, 2016), principalement en raison de déficiences comportementales observées chez les individus d'élevage, naïfs vis-à-vis des prédateurs (Rantanen et al., 2010b, 2010a; Sokos et al., 2008; mais aussi physiologiques, morphologiques, et génétiques, voir Bro, 2016; Champagnon, Guillemain, et al., 2012; Homberger et al., 2013; Putaala & Hissa, 1995; Liukkonen-Anttila, Saartoala, & Hissa, 2000).

Le recours aux oiseaux d'élevage apparaît bien souvent comme la seule alternative possible au renforcement ou à la réintroduction de populations d'oiseaux (voir Buner et al., 2011 pour la Perdrix grise; et Fischer & Lindenmayer, 2000 pour une revue des translocations d'espèces d'oiseaux impliquant à 84% des individus d'élevage). Cependant, leur utilisation est identifiée comme une cause majeure d'échec d'opérations de translocation (Fischer & Lindenmayer, 2000; Griffith et al., 1989; Sokos et al., 2008). La capacité d'ajustement comportemental aux perturbations environnementales observées à partir de nos résultats (Chapitres III & IV), suggère que certains individus d'élevage sont en mesure de répondre aux perturbations environnementales. Favoriser cette capacité d'ajustement permettrait d'augmenter la survie post-lâcher des individus. L'« ensauvagement » pourrait constituer une piste d'amélioration efficace (au moins à court terme), de la survie post-lâcher des oiseaux issus de reproduction en captivité (Sokos et al., 2008), impliquant : l'utilisation de larges volières (avec végétation naturelle), une alimentation au sol réalisée de manière imprévisible (Homberger, Jenni, Duplain, Lanz, & Schaub, 2014), une minimisation du contact humain (R. B. Jones & Waddington, 1992), et un entraînement anti-prédateur avant le lâcher (Beani & Dessì-Fulgheri, 1998; Gaudio et al., 2011; Griffin et al., 2000; Sánchez-García et al., 2016; van Heezik, Seddon, & Maloney, 1999).

La diversification des populations sources pourrait également être envisagée lors des translocations afin de diversifier les conditions d'élevages et pools génétiques des individus, diversifiant en conséquence les types comportementaux (personnalités), les paramètres génétiques, immunogénétiques et physiologiques pour maximiser les capacités d'ajustement et d'adaptation des populations lâchées face aux pressions et stress environnementaux (Ewen et al., 2012; Keller et al., 2012; Smith & Blumstein, 2008; Watters & Meehan, 2007).

5. *Comment s'y prendre ? Quels moyens mettre en œuvre ?*

À ce jour, malgré les nombreux oiseaux lâchés annuellement (Bro, 2016; SNPGC, s. d.), l'espèce Perdrix grise est toujours en déclin et continue de disparaître localement (Chapitre I ; Comolet-Tirman et al., 2015). Initialement développée pour inciter les chasseurs à gérer leurs territoires et les populations d'espèces d'intérêt cynégétique, la pratique de gestion par lâchers cynégétiques annuels d'oiseaux d'élevage arrive à un point de rupture (Bro, Mayot, et al., 2006; ONCFS, 2014; Sokos et al., 2008). Madden et al. (2018) relèvent que 60% des Faisans de Colchide lâchés annuellement au Royaume-Uni, soit 21 millions d'individus, ne sont finalement pas prélevés par les chasseurs, représentant un manque à gagner annuel de 270 millions de livres sterling (soit environ 310 millions d'euros) pour les chasseurs. En France, le Syndicat National de Production des Gibiers de Chasse (qui représente 70% de la production française de gibier, SNPGC, s. d.), comptabilise 14 millions de Faisans de Colchide, et 5 millions de Perdrix (grise et rouge) produits chaque année pour le territoire français. Si l'on fait l'hypothèse restrictive que ces chiffres représentent le nombre d'oiseaux lâchés annuellement en France (sans tenir compte des 30% non produits par le SNPGC), et que les taux de retour (nombre de prélèvements par les chasseurs par rapport au nombre d'oiseaux lâchés) s'établissent non pas à 60% mais à 50% (en cohérence avec les taux de retour observés sur l'une des ACCA de notre zone d'étude pour les Perdrix grise et rouge : 48% en 2013, 60% en 2014, 35% en 2015), le manque à gagner annuel pour les chasseurs serait estimé à 16 millions d'euros pour les Perdrix ($6,5\text{€} \times 2,5$ millions d'oiseaux), et 56 millions d'euros pour le Faisan ($8\text{€} \times 7$ millions d'oiseaux), soit un total de 72 millions d'euros par an en France.

Cette estimation soutient l'idée que ce type de gestion n'est profitable ni aux chasseurs (perte économique : Chapitre I ; Madden et al., 2018; déconnexion de la pratique traditionnelle de la chasse : Sokos et al., 2008; pourrait bénéficier aux populations de prédateurs et alimenter les conflits homme-faune : Bicknell et al., 2010; Bro, Arroyo, et al., 2006; Kenward, Hall, Walls, & Hodder, 2001; Viñuela & Arroyo, 2002), ni aux populations renforcées (Madden et al., 2018; Sokos et al., 2008). L'étude de Delibes-Mateos et al. (2014) menée en Espagne, montre que certains chasseurs sont conscients de la dégradation de leur territoire de chasse et seraient prêts à payer pour améliorer les caractéristiques écologiques de ces territoires (retrouver une plus grande diversité d'espèces de gibier, des populations sauvages, des couverts végétaux naturels). Cette perception rejoint certaines préoccupations

formulées par les chasseurs sur notre zone d'étude (observations personnelles), s'alarmant de la dérive vers une pratique de la chasse qui ne correspond plus à leurs attentes, c'est-à-dire à la pratique traditionnelle de la chasse (voir aussi Sokos et al., 2008). Nous défendons l'idée que la pratique de gestion cynégétique mixte devrait être reconsidérée dans un cadre de conservation (voir aussi Sokos et al., 2008), en s'imprégnant des principes et connaissances acquises de biologie de la réintroduction (WPA-IUCN, 2009), dans le but de rétablir des populations viables. Par conséquent, nous préconisons d'orienter les réflexions vers les mesures suivantes :

- (1) Réaliser une étude économique fine, afin de quantifier la perte monétaire liée à cette pratique de gestion et préconiser une réallocation des moyens vers des mesures de gestion permettant d'améliorer l'habitat (mesures agro-environnementales pouvant mener à une augmentation du succès reproducteur, voir Homberger, Duplain, Jenny, & Jenni, 2017; maintien de chaumes, cultures à gibier, couverts permanents, habitats non-cultivés, voir Buner, 2009; R. J. Fuller, Hinsley, & Swetnam, 2004), et la qualité des oiseaux lâchés (sauvages, oiseaux d'élevage « ensauvagés », entraînés contre les prédateurs)
- (2) Mettre en place des plans de chasse permettant de limiter le dérangement, les pressions, et d'assurer la réimplantation de populations viables (voir Mérieau & Bro, 2009)
- (3) Engager une réflexion territorialisée des espèces à lâcher sur la base de considérations écologiques, et mutualiser ces réflexions en intégrant l'ensemble des espèces de gibier afin d'optimiser les moyens techniques, financiers, et l'efficacité des programmes (diagnostics du territoire, propositions de gestion, suivis) (voir Champagnon, Elmberg, et al., 2012)
- (4) Développer des outils de suivi et de diagnostic post-lâcher de ces opérations qui restent à ce jour difficilement quantifiables (Champagnon, Elmberg, et al., 2012; Laikre et al., 2006) : permettre la traçabilité des opérations (origine des oiseaux, destination, nombre d'oiseaux impliqués) et la distinction entre les oiseaux lâchés et sauvages (ou reproduits en nature) par le baguage systématique (voir aussi Champagnon, Elmberg, et al., 2012; Laikre et al., 2006), ainsi que l'évaluation et la quantification du succès des opérations (suivis post-lâchers) (voir aussi Buner, 2009). Ces mesures permettront

également d'améliorer les connaissances autour de ces pratiques de lâcher, et de mieux estimer les tendances démographiques des populations sauvages prises en compte dans l'établissement des statuts de conservation (Comolet-Tirman et al., 2015).

Seule la création d'une synergie entre chasseurs, agriculteurs, gestionnaires et scientifiques permettra cette mutation vers une gestion intégrée et territorialisée des populations.

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Titre : Survivre en agrosystème céréalier – le défi de la Perdrix grise : sélection d'habitat, compétition interspécifique et traits individuels

Mots clés : Ecologie, Compétition interspécifique, Paysages agricoles, Perdrix grise, Pratiques cynégétiques, Pressions naturelles et anthropiques, Sélection d'habitat, Traits individuels

Résumé : La sélection de l'habitat est définie comme un processus comportemental en réponse à des stimuli environnementaux tels que la disponibilité en ressources (alimentation, refuges) et la présence de menaces (compétiteurs, prédateurs). La compréhension des mécanismes sous-jacents est essentielle en écologie et permet d'identifier et d'appréhender les facteurs limitant les populations. L'enjeu de cette thèse était d'identifier les facteurs limitants (paysages, pratiques cynégétiques) et la réponse des populations de Perdrix grise (*Perdix perdix*) soumises à gestion cynégétique (apports annuels d'oiseaux d'élevage, sans arrêt de la chasse). Les patrons de sélection d'habitat ont varié vers un évitement moins prononcé des habitats associés à un fort risque de prédation, dans le même temps que la qualité d'habitat a diminué et que la

prévalence d'oiseaux d'élevage a probablement augmenté dans la population. La compétition interspécifique avec la Perdrix rouge affecte également la sélection de l'habitat de la Perdrix grise. Certains individus démontrent une capacité d'ajustement comportemental (rythme d'activité, sélection de l'habitat, de l'espace) à la structuration du risque au cours du cycle circadien, possiblement influencée par des déterminants individuels (personnalité, état sanitaire). La qualité d'habitat, les pressions de prédation et de chasse sont des facteurs structurants des populations. Une gestion cynégétique basée sur l'apport d'oiseaux naïfs et d'espèces compétitrices, un dérangement lié à la chasse en phase post-lâcher et une non-évaluation préalable de la qualité de l'habitat, rendent le maintien des populations de Perdrix grise sur un territoire très incertain.

Title: Surviving in cereal agrosystems – the grey partridge's challenge: habitat selection, interspecific competition and individual traits

Keywords: Agricultural landscapes, Ecology, Game practices, Grey partridge, Habitat selection, Individual traits, Interspecific competition, Natural and human disturbances

Abstract: Habitat selection is a behavioural process in response to environmental stimuli as resource availability (food, shelter) and threats (competitors, predators). The understanding of the underlying mechanisms is crucial in ecology and allow to identify and consider factors limiting populations. The stake of this PhD thesis was to identify limiting factors (landscapes, game practices) and responses of grey partridge (*Perdix perdix*) populations under mixed game management (annual releases of captive-reared birds, without shooting suspension). Habitat selection patterns have changed towards a lower avoidance of risky habitats, while habitat suitability has decreased and the proportion of captive-reared birds in the population has likely increased.

Interspecific competition with red-legged partridge also affected habitat selection in grey partridge. Some individuals showed a behavioural capacity to adjust (in terms of rhythms of activity, habitat selection, space use) to the spatiotemporal structuration of risk along the diel cycle, potentially influenced by individual traits (personality, health status). Habitat suitability, predation and hunting pressures were identified as structuring factors of grey partridge populations. A game management based on releases of naïve birds and competing species, disturbances induced by shooting during the post-release period, and no preliminary assessment of habitat quality, could locally imperil the maintenance of grey partridge populations.