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DÉTERMINANTS COMPORTEMENTAUX DE LA RÉPARTITION SPATIALE DES OISEAUX DANS LES FORÊTS FRAGMENTÉES

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Résumé court

L’objectif de cette étude était de déterminer si la sensibilité à la structure des forêts observée chez plusieurs espèces de migrateurs Néotropicaux est reliée à leur comportement. Plus spécifiquement, j’ai mesuré la force de la relation entre la sensibilité à la structure des forêts des oiseaux forestiers et deux facteurs comportementaux : la réticence à traverser les milieux ouverts et la tendance à agréger les territoires. Les variations observées entre les espèces ont été mises en relation avec la sensibilité à la structure des forêts de ces mêmes espèces. Je montre que les espèces varient dans leur réticence à traverser les milieux ouverts et dans leur tendance à regrouper leurs territoires. Cependant, les variations entre les espèces ne permettent pas de prédire la sensibilité à la structure des forêts telle que mesurée par la probabilité d’occurrence. Mais la conservation de boisés de grande superficie pourrait servir à maintenir les espèces regroupant leurs territoires.

Résumé long

La perte et la fragmentation des forêts à l'échelle du paysage sont généralement considérées comme étant des facteurs majeurs du déclin des populations de migrateurs Néotropicaux. Bien que la sensibilité à la structure des forêts ait été identifiée chez de nombreuses espèces, les mécanismes sous-jacents restent peu connus. Cette situation empêche les chercheurs de prédire quelles espèces seront affectées négativement par la perte et la fragmentation des forêts et d'identifier les espèces à risque. L'objectif général de cette étude était de déterminer si la sensibilité à la structure des forêts est reliée au comportement des espèces. Plus spécifiquement, cette étude comportait deux objectifs principaux. Le premier objectif consistait à analyser la force de la relation entre la sensibilité à la structure des forêts et deux facteurs comportementaux: la réticence à traverser les milieux ouverts et la tendance à agréger les territoires. La majorité des espèces avaient tendance à regrouper leurs territoires. De plus, les espèces variaient dans leur réticence à traverser les milieux ouverts. Par contre, les variations de ces comportements entre les espèces ne permettaient pas de prédire la sensibilité à la structure des forêts. Le deuxième objectif comprenait l'étude approfondie de l'effet de la présence des conspécifiques sur la sélection de l'habitat de reproduction de la Paruline couronnée (*Seiurus aurocapilla*). Chez cette espèce, la présence et le nombre des conspécifiques n'influençaient pas la probabilité de colonisation des territoires par les individus sans territoires. Par contre, l'analyse de données publiées montrait que les femelles Paruline couronnée s'installent préférablement dans les populations avec des densités élevées de mâles territoriaux, indépendamment de la perte et de la fragmentation des forêts. En conclusion, la conservation de parcelles de forêt de grande superficie pourrait être essentielle au maintien des espèces au statut préoccupant qui ont tendance à regrouper leurs territoires.

Abstract

Forest loss and fragmentation at the landscape scale are generally considered to be major causes of the reported declines in many Neotropical migratory birds. Even though sensitivity to landscape structure has been identified in numerous species, the underlying mechanisms remain poorly understood. This situation keeps researchers from predicting which species are most likely to be negatively affected by fragmentation and from identifying species at risk before the onset of forest loss and fragmentation. The main purpose of this study was to determine whether sensitivity to landscape structure could be explained by behavioural processes. More specifically, there were two main objectives in this study. The first objective consisted of analyzing the strength of the relationship between sensitivity to landscape structure and two behavioural processes: the reluctance to cross open areas and the tendency to aggregate territories. The majority of the species that were studied aggregated their territories. Furthermore, species varied in their reluctance to venture into open habitat. However, variations in these behaviours among species could not help predict sensitivity to landscape structure. The second objective involved studying the effect of conspecific presence on the selection of breeding habitat in the Ovenbird (*Seiurus aurocapilla*). Moreover, the presence and number of Ovenbird conspecifics did not influence the probability of territory settlement by Ovenbird floaters. On the other hand, the analysis of published data showed that Ovenbird females preferably settle in high-density populations, even after accounting for forest fragmentation. In conclusion, the conservation of large forest patches could be essential to maintain populations of species of conservation concern that tend to aggregate their territories.

Avant-Propos

Et tamen minimum quod potest haberi de cognitione rerum altissimarum, desiderabilius est quam certissima cognitio quae habetur de minimis rebus

Saint Thomas d'Aquin, Summa Theologica I, 1, 5 ad 1

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Introduction générale

En écologie forestière, les études portant sur les effets de la fragmentation des forêts sur les populations animales sont abondantes et variées. Le terme ‘fragmentation’ est ubiquiste et fermement incorporé dans la littérature scientifique. Ce terme est souvent utilisé pour décrire une situation où le nombre des parcelles d’habitat diminue et où l’isolement des parcelles résiduelles augmente (e.g. Diffendorfer et al. 1995; Robinson et al. 1995). Or, ces caractéristiques peuvent servir à définir des paysages qui connaissent uniquement une réduction de leur couvert forestier sans que le degré de fragmentation n’augmente (Fahrig 1997). En effet, la fragmentation modifie la configuration des parcelles de forêt en augmentant le ratio périmètre/surface de ces parcelles. Par contre, la perte de couvert forestier dans un paysage peut se traduire par une réduction du nombre des parcelles sans que la configuration des parcelles ne soit altérée. De même, si certaines parcelles de forêt sont converties en milieu ouvert, l’isolement entre les parcelles résiduelles de forêt augmentera mais la fragmentation ne sera pas en cause. La perte d’habitat et la fragmentation vont généralement de pair, ce qui explique pourquoi les paysages avec de petites parcelles de forêt isolées sont généralement considérés comme étant fragmentés. Cependant, ces paysages représentent un scénario extrême dans le gradient possible de perte et de fragmentation des forêts. L’isolement des parcelles de forêt ne survient que lorsque la perte du couvert forestier est devenue extensive. Au début de la transformation des forêts continues, le couvert forestier est plutôt perforé (*sensu* Forman et Godron 1986; Feinsinger 1997) et continue à être connecté de façon importante. Mais, même à cette étape, la fragmentation modifie la configuration du couvert forestier.

De nombreuses études montrent que la présence et la densité des populations d’espèces animales sont généralement moins élevés dans les petits fragments forestiers isolés que dans les forêts continues (Robbins 1979; van Dorp et Opdam 1987; Blake 1991). Cet effet de la perte et de la fragmentation des forêts sur la répartition des populations est particulièrement marqué dans les paysages où la proportion de couvert forestier est très faible. En effet, lorsque la proportion de couvert forestier est au delà d'un seuil 20-30% du paysage, la probabilité de présence des espèces semble être associée de façon linéaire à la quantité de forêt résiduelle. Sous ce seuil, la probabilité d’occurrence est plus faible (Andrén 1994; Bender et al. 1998) et le risque d’extinction locale est plus élevé (Fahrig 1997; 2002) que ce qui serait prédit basé sur la quantité de forêt. Il semble donc que la diminution du nombre d’espèces dans un paysage fragmenté soit imputable à autre chose qu’à la simple perte d’habitat. Cette situation a amené les chercheurs à se questionner sur l’importance de la configuration de la forêt sur la répartition des espèces (revu dans Freemark et Collins 1992). En fait, plusieurs variables de configuration de la forêt telles que la longueur des lisières et la superficie de forêt d’intérieur ont été associées à l’occurrence des espèces (Drolet et al. 1999; Villard et al. 1999).

Depuis plusieurs années, les oiseaux forestiers servent d’organismes modèles pour étudier les conséquences de la perte et de la fragmentation des habitats forestiers sur la répartition des individus (e. g. Ambuel et Temple 1983; Temple et Cary 1988; Verboom et al. 1991; Villard et al. 1995; Boulinier et al. 1998; Zanette et al. 2000). Ces études portant sur les populations aviaires en milieu fragmenté ont remarqué un phénomène important : certaines espèces semblent systématiquement absentes de parcelles de forêt isolées, même si ces parcelles seraient assez grandes pour contenir leurs territoires (Forman et al. 1976; Galli et al. 1976; MacClintock et al. 1977; Whitcomb et al. 1977; Robbins 1979; Whitcomb et al. 1981;

Opdam et al. 1984). Ces espèces qui se retrouvent moins souvent dans les petites parcelles de forêts isolées que dans des parcelles de superficie semblable en forêt continue sont donc désignées comme étant sensibles à la structure des forêts (Koford et al. 1994).

'Sensibilité' à la structure des forêts

Tout au long de cette thèse, l'expression 'sensibilité à la structure des forêts' servira à désigner les espèces qui se retrouvent moins souvent ou qui sont moins abondantes dans les petits fragments isolés que ce qui serait prédit basé sur la quantité de forêt disponible. Plusieurs chercheurs ont documenté la sensibilité à la structure des forêts chez les espèces d'oiseaux (Wiens 1994; Villard et al. 1995; Flather et Sauer 1996; Hagan et al. 1996; Schmiegelow et al. 1997; Mazerolle et Villard 1999; Hobson et Bayne 2000). La réponse à la structure des forêts semble constante entre les années (Desrochers données non publiées) et spécifique à chaque espèce (Freemark et Collins 1992).

Les études sur la répartition des espèces aviaires en milieu fragmenté s'inscrivent dans le contexte où un apparent déclin généralisé des populations des migrateurs Néotropicaux alarme plusieurs auteurs (Tableau 1; Robbins et al. 1989; Askins et al. 1990; Opdam 1991). Ce déclin est maintenant contesté (James 1998) mais a inspiré pendant une vingtaine d'années de nombreuses études sur ses causes potentielles (Lens et Dhondt 1994; McGarigal et McComb 1995; Machtans et al. 1996; Bender et al. 1998; Robinson et al. 1995; Burke et Nol 1998; Huhta et al. 1999; Villard et al. 1999). Ces causes sont encore peu connues mais les événements survenant dans les aires de reproduction semblent importants pour la viabilité des populations aviaires. En effet, plusieurs auteurs ont observé une corrélation positive entre le succès reproducteur et le recrutement de nouveaux individus dans la population l'année suivante (Nolan 1978; Virolainen 1984; Holmes et al. 1992; Sherry et Holmes 1992). Puisque le nombre et la densité des populations d'espèces d'oiseaux sont généralement moins élevés dans les petits fragments forestiers isolés que dans les forêts continues, il s'ensuit que les changements de configuration des forêts sont considérés par plusieurs comme étant un des facteurs majeurs du déclin des populations (Robinson et al. 1995, Donovan et Flather 2002).

Bien que la sensibilité à la structure des forêts et le déclin des populations aient été identifiés chez de nombreuses espèces (Tableau 1), la relation entre ces deux phénomènes reste inexpliquée. Cette situation empêche les chercheurs de prédire quelles espèces seront affectées négativement par la perte et la fragmentation de l'habitat et d'identifier les espèces à risque. Néanmoins, plusieurs mécanismes ont été suggérés pour expliquer la relation entre la sensibilité à la structure des forêts et le déclin des populations. La plupart de ces mécanismes peuvent être classés en deux grandes catégories : les évènements survenant avant ou après la colonisation de l'habitat de nidification des individus.

Tableau 1. Proportion d’espèces forestières dont les populations ont significativement (alpha = 0,05) diminué. Tiré de Sauer et al. (2004).

Espèce (*nom scientifique*)	1966-2003	1980-2003
Espèces nichant dans la strate arbustive	36% (n = 87)	36% (n = 87)
Espèces nichant en cavité	18% (n = 62)	23% (n = 62)
Espèces ayant des nids ouverts	38% (n = 182)	42% (n = 182)
Migrateurs Néotropicaux	33% (n = 137)	38% (n = 137)
Migrateurs sur courtes distances	37% (n = 106)	45% (n = 106)
Résidents permanents	23% (n = 93)	26% (n = 93)
Espèces forestières	24% (n = 131)	33% (n = 131)
Espèces nichant près du sol	48% (n = 112)	47% (n = 112)
Espèces nichant dans la futaie	24% (n = 124)	31% (n = 124)

Avant la colonisation de l’habitat de nidification, les individus doivent pouvoir explorer les sites potentiels et évaluer la qualité des ressources disponibles. Il s’ensuit que si les oiseaux sont réticents à traverser les milieux ouverts (Lens et Dhondt 1994; Bélisle 2000), milieux qui sont prédominants dans les paysages de forêt fragmentée, les oiseaux forestiers coloniseront moins souvent les parcelles de forêt isolées. Cette situation pourrait expliquer les densités de population plus faibles dans les paysages connaissant une perte importante de couvert forestier. D’un autre côté, si les mouvements sont libres de contrainte, les individus établiront alors leur territoire en fonction de la qualité apparente de l’habitat. Or, si les ressources nécessaires sont perçues par les oiseaux comme étant moins présentes en milieu fragmenté, certaines espèces d’oiseaux forestiers pourraient éviter activement ces milieux et s’installer préférablement en forêt continue (Burke et Nol 1998; Huhta et al. 1998; Zanette et al. 2000).

Après la sélection du territoire de nidification, la qualité réelle des habitats influencera le succès reproducteur en milieu fragmenté. Par exemple, la prédation (Gates et Gysel 1978; Andrén 1992; Roberts et Norment 1999) et le parasitime des nids (Temple et Cary 1988; Askins 1995; Donovan et al. 1997; Robinson et al. 1995) sont plus importants en milieu fragmenté qu’en forêt continue. De plus, la quantité de nourriture disponible est plus faible dans les paysages fragmentés (Burke et Nol 1998; Zanette et al. 2000), ce qui pourrait réduire la condition physique des oisillons. La perte et de la fragmentation pourrait donc influencer indirectement les niveaux de populations si le succès reproducteur en milieu fragmenté n’est pas assez important pour compenser la mortalité des adultes (Temple et Cary 1988; Roth et Johnson 1993; Desrochers 2003). Les effets de la qualité réelle de l’habitat sur le succès reproducteur surviennent surtout après que les adultes aient sélectionné leur territoire de nidification. Or, cette thèse porte sur les effets de la perte et de la fragmentation des forêts sur la sélection de l’habitat des passereaux forestiers. Les évènements survenant après la sélection des territoires ne seront donc pas étudiés dans cette thèse.

L’étude du comportement aviaire à l’échelle du paysage

Malgré l’importance potentielle des comportements survenant avant la colonisation sur la répartition des oiseaux, le comportement des individus reste rarement incorporé dans les études portant sur les effets de la perte d’habitat (Stutchbury 1998; Bélisle et al. 2001; Norris et Stutchbury 2002). Cela est probablement dû au fait que les études quantifiant le comportement d’individus sont généralement effectuées à des échelles spatiales différentes des études sur la sensibilité à la structure des forêts (Lima et Zollner 1996). Ainsi, une meilleure compréhension de la répartition des populations aviaires pourrait être réalisée en étudiant ces comportements à des échelles spatiales comparables. Dans cette thèse, j'étudie deux comportements survenant avant la reproduction pouvant expliquer la sensibilité à la structure des forêts des espèces forestières (Lima et Zollner 1996; Walters 1998; Desrochers 2003). Ces comportements sont 1) la dispersion et 2) l'attraction conspécifique.

La dispersion

Des études récentes ont démontré que les milieux ouverts peuvent constituer des barrières aux mouvements d'oiseaux forestiers (Sieving et al. 1996; Desrochers et al. 1999; Bélisle et Desrochers 2002). Ainsi, plusieurs espèces semblent réticentes à traverser les milieux ouverts. Il peut sembler surprenant que des organismes ayant les capacités physiques nécessaires pour migrer sur des milliers de kilomètres soient contraints par des milieux ouverts de quelques dizaines de mètres. Cependant, les mouvements associés à la migration et ceux associés aux mouvements à petite échelle résultent de différentes motivations (Villard et al. 1995). Lors des mouvements à petite échelle, les coûts associés à se déplacer en milieu ouvert sont probablement différents de ceux associés aux mouvements sous couvert forestier. Par exemple, il se pourrait que les coûts énergétiques associés aux déplacements dans les milieux ouverts soient plus élevés que les déplacements sous couvert forestier (Matthysen et Currie 1996). De plus, il est possible que la vulnérabilité aux prédateurs augmente dans les milieux ouverts (Lima et Dill 1990). Les mouvements des oiseaux à petite échelle pourraient se transposer sur leur répartition à grande échelle. En effet, si les oiseaux sont réticents à traverser les milieux ouverts pendant leurs mouvements exploratoires, les parcelles de forêt les plus isolées pourraient ne pas être colonisées. Des différences entre les espèces dans les capacités de se déplacer pourraient donc expliquer les variations de sensibilité à la structure des forêts observées entre les espèces (Walters 1998). Il se pourrait également que, pour une même espèce, les mâles et les femelles réagissent différemment aux milieux ouverts. Si les déplacements des femelles sont plus sujets à être contraints par les milieux ouverts, cela pourrait se traduire par un taux d'appariement plus faible dans les parcelles de forêt isolées (Cooper et Walters 2002).

L'attraction conspécifique

Traditionnellement, les voisins de la même espèce, ou voisins conspécifiques, ont été considérés uniquement comme des compétiteurs pour les ressources limitées de l'habitat telles la nourriture, les perchoirs et les sites de nidification (Rosenzweig 1985; Fretwell et Lucas 1970; Fretwell 1972). Cependant, les individus de certaines espèces dites 'non-coloniales' s'installent préférablement près de conspécifiques (Alatalo et al. 1982; Stamps 1987; 1988; Minchington 1997; Muller et al. 1997; Etterson 2003; Doligez et al. 2004; Ward et Schlossberg 2004). Ce phénomène intriguant demeure cependant peu documenté et pourrait se produire chez de nombreuses espèces. Les études traitant d'attraction conspécifique suggèrent souvent que la présence de conspécifiques pourrait conférer des avantages aux nouveaux arrivants comme une meilleure protection contre les prédateurs (Perry et Andersen 2003) ou un succès reproducteur plus élevé (Stamps 1994). La présence de voisins conspécifiques pourrait ainsi être un critère de valeur de l'habitat utilisé par les espèces lors de la sélection de leur territoire de nidification (Wander 1985). Cette situation pourrait potentiellement mener à une contagion de la répartition des espèces, associée à une sous-utilisation de parcelles de superficie trop faible pour accommoder plusieurs territoires. Cette idée n'est pratiquement pas véhiculée dans la littérature actuellement. Par contre, des modèles théoriques suggèrent que l'absence de voisins conspécifiques devrait diminuer la probabilité de recolonisation d'une parcelle après une extinction locale (Smith et Peacock 1990; Lima et Zollner 1996). L'attraction conspécifique pourrait contribuer à diminuer la viabilité des populations, puisque plusieurs parcelles d'habitat convenable resteraient alors inoccupées.

Ray et al. (1991) ont d’ailleurs incorporé l’attraction conspécifique dans des modèles de métapopulation. Leurs résultats indiquent que l’attraction conspécifique pourrait potentiellement diminuer la proportion de parcelles occupées dans un paysage. Si c’est le cas, les espèces qui ont tendance à regrouper leurs territoires devraient également être celles qui tendent à être absentes en milieu fragmenté.

Objectifs de l’étude et organisation de la thèse

Dans cette thèse, j’étudie les facteurs comportementaux qui pourraient être associés à la sensibilité à la structure des forêts observée chez plusieurs espèces de migrateurs Néotropicaux retrouvés en forêt. Les facteurs comportementaux sont étudiés sur un territoire de 1200 km^2 situé dans les comtés de Beauce et Bellechasse, au sein de la vallée du St-Laurent. L’aire d’étude est localisée dans un paysage à forte dominance agricole où la perte et la fragmentation des forêts est importante et bien documentée (Desponts 1995, Robitaille et Saucier 1998). Dans l’aire d’étude, la conversion d'habitats forestiers en milieux agricoles a été modelée de façon distinctive par le système seigneurial. En effet, au cours des ans, le défrichage s’est progressivement éloigné de routes parallèles pour laisser intactes de longues bandes de forêt (Fig. 1). Ce morcellement du couvert forestier au sein de la vallée du Saint-Laurent ne s’est pas encore traduit par la multiplication de petites parcelles de forêt isolées. Ceci ne correspond pas à ce qui est observé dans de nombreux paysages agricoles utilisés pour étudier les effets de la fragmentation sur les populations animales (Robinson et al. 1995; Burke et Nol 1998; Huhta et al. 1999; Villard et al. 1999). Néanmoins, l’aire d’étude sélectionnée montre une perte sérieuse du couvert forestier (Desponts 1995) et un ratio périmètre/surface élevé des parcelles de forêt. Dans ce contexte, les effets de la fragmentation sur les comportements aviaires devraient pouvoir être identifiés et mesurés. En effet, des études préalables dans la même aire d’étude ont détecté des contraintes dans les mouvements de nombreuses espèces d’oiseaux forestiers (Bélisle 2000).

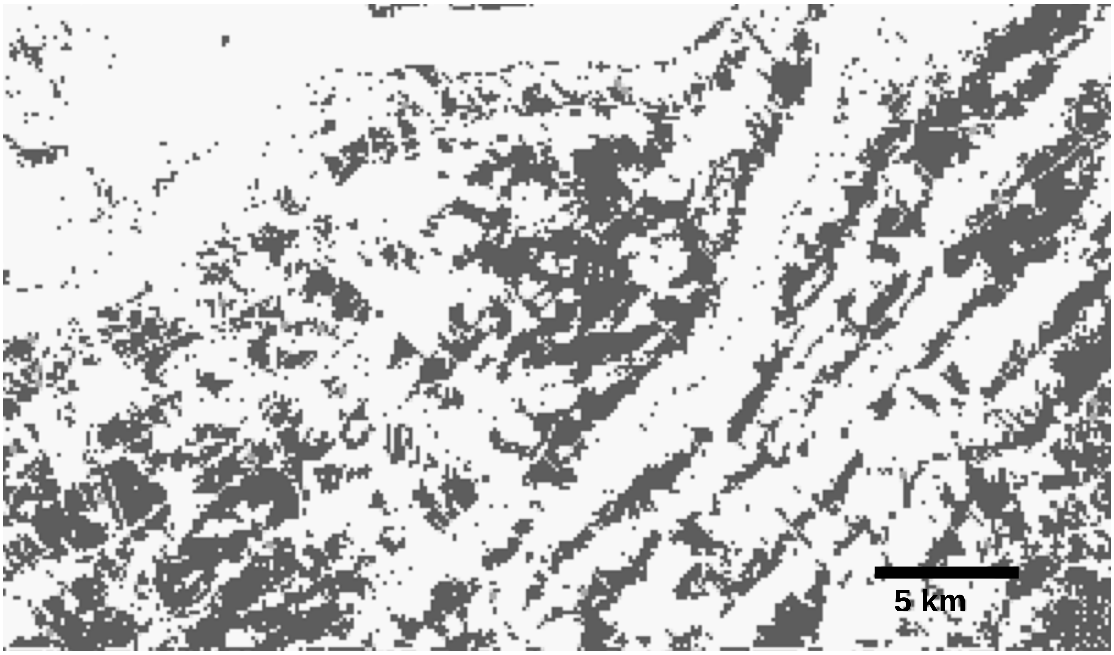

Figure 1. Distribution de la forêt mature (zones grises) en 1993-1994 telle que classifiée par une image satellite. Québec (46° 45’ N, 71° 20’ O), Québec, Canada, est située dans le coin supérieur gauche de la carte.

La thèse est divisée en cinq chapitres rédigés sous la forme d’articles scientifiques. Chaque chapitre se traduit par un objectif distinct. Les premiers chapitres ont pour objectif d’analyser la force de la relation entre la sensibilité à la structure des forêts et différents facteurs comportementaux. Dans ces premiers chapitres, l’utilisation de la méthode comparative me permet d’aller au-delà de la simple documentation de l’existence des comportements étudiés. Dans le chapitre un, je calcule un indice de sensibilité des espèces à la structure des forêts, soit la probabilité d’occurrence en milieu fragmenté. De plus, à partir d’essais comportementaux, j’identifie les espèces qui sont réticentes à traverser les milieux ouverts lors de leurs déplacements à petite échelle. Je quantifie enfin la force de la relation entre la réticence aux milieux ouverts et le degré de sensibilité à la structure des forêts. Dans le deuxième chapitre, je valide la méthodologie utilisée au premier chapitre pour mesurer la réticence à traverser les milieux ouverts. Au chapitre trois, je mesure le degré de contagion dans la répartition des oiseaux forestiers comme cause potentielle de sensibilité à la structure des forêts. Le degré de contagion est mesuré à différentes échelles spatiales tout en contrôlant les effets associés à la végétation. Je calcule ensuite la relation entre la tendance à regrouper les territoires et la probabilité d'occurrence en milieu fragmenté. L'objectif des quatrième et cinquième chapitres comprenait l'étude approfondie de l'effet de la présence des conspécifiques sur la sélection de l'habitat de reproduction de la Paruline couronnée (*Seiurus aurocapilla*). J'ai sélectionné la Paruline couronnée car : 1) elle est réputée sensible à la superficie et à la structure des forêts (Ortega et Capen 1999); 2) les mâles sont territoriaux et cette espèce est relativement abondante dans l'aire d'étude (M. Bélisle, communication personnelle); et 3) de nombreuses études ont examiné les effets de la perte d'habitat sur la démographie de la Paruline couronnée. Dans le quatrième chapitre, je présente une expérience afin de tester l'importance de la présence des voisins conspécifiques sur la colonisation des territoires des mâles Paruline couronnée. Dans le cadre de cette expérience, je manipule les nombres de mâles Paruline couronnée dans différents sites en milieu naturel et j'analyse le taux de remplacement de mâles retirés en fonction de la présence de mâles résiduels. Dans le dernier chapitre, je mesure l'influence de la densité des mâles Paruline couronnée sur l'établissement des femelles. Pour ce faire, j'effectue une revue de littérature afin de quantifier la relation entre le succès d'appariement et la densité des mâles tout en tenant compte de la perte et de la fragmentation de l'habitat.

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Chapitre 1

Relationships between gap-crossing abilities and landscape use in forest birds

Bourque, J. et A. Desrochers. **Relationships between gap-crossing abilities and landscape use in forest birds.** Sera soumis à *Oikos*. Centre de recherche en biologie forestière, Pavillon Abitibi-Price, Université Laval, Québec, Qc, G1K 7P4, Canada. *Ce chapitre est le fruit du travail du candidat. André Desrochers a participé à l'élaboration de l'idée de base de ce chapitre.*

Résumé

La réticence à se déplacer en milieu inhospitalier est une théorie fréquemment invoquée pour expliquer la sensibilité à la structure des forêts chez les populations aviaires. Nous avons testé si des variations dans la réticence à traverser les milieux ouverts pouvaient expliquer les différences de sensibilité à la structure des forêts chez les espèces forestières. Nous avons calculé un indice de la sensibilité à la structure des forêts à partir de données d'occurrence pour dix passereaux forestiers. Pour chaque espèce, nous avons aussi calculé un indice de réticence à traverser les milieux ouverts. Nous avons tenu compte des effets phylogénétiques et analysé la relation entre les deux indices. Nous avons prédit que les espèces répondant le plus négativement à la perte et à la fragmentation des forêts seraient les plus réticentes à traverser les milieux ouverts. La paruline couronnée (*Seiurus aurocapilla*) était l'espèce la plus sensible à la structure des forêts tandis que la paruline flamboyante (*Setophaga ruticilla*) était l'espèce la moins sensible. La paruline à tête cendrée (*Dendroica magnolia*) et le viréo aux yeux rouges (*Vireo olivaceus*) étaient les espèces les plus réticentes à traverser les milieux ouverts. Cependant, la réticence à traverser les milieux ouverts des espèces étudiées n'a pas permis de prédire leur sensibilité à la structure des forêts. Nous suggérons donc que des facteurs autres que la mobilité pourraient mieux expliquer les patrons d'occurrence des oiseaux forestiers.

Abstract

Reluctance to venture into inhospitable habitat is a frequent explanation for the apparent sensitivity of birds to landscape structure. We tested whether variations in species' ability to cross open habitat are associated with observed differences in landscape sensitivity in forest birds. We calculated an index of landscape sensitivity from presence-absence data for ten forest-dwelling species. For each species, we also used playbacks to calculate an index of reluctance to cross gaps in the canopy. We controlled for possible phylogenetic effects and analyzed the relationship between the two indices. We predicted that the species responding most negatively to forest loss and associated fragmentation would be the most reluctant to cross gaps in the forest cover. Ovenbirds (*Seiurus aurocapilla*) was the species most sensitive to landscape structure while American redstarts (*Setophaga ruticilla*) responded positively to forest loss and fragmentation. Magnolia warblers (*Dendroica magnolia*) and red-eyed vireos (*Vireo olivaceus*) were the species most reluctant to cross gaps. The reluctance to cross gaps in the forest cover was not useful in predicting landscape sensitivity. We suggest that processes other than dispersal ability may better explain occurrence patterns in forest birds.

INTRODUCTION

In agricultural landscapes, forest songbirds are often absent from small forest fragments even though these seemingly suitable habitats may be large enough to accommodate territories (Robbins 1979; van Dorp and Opdam 1987; Blake 1991). Species that occur less frequently or in lower density in small habitat fragments can be termed sensitive to landscape structure (Freemark and Collins 1992; Villard 1998). Thus far, researchers have investigated the role of several correlates of landscape sensitivity including (1) local factors such as decreases in food abundance (Burke and Nol 1998) or increased threats to nesting success (Robinson et al. 1995; Roberts and Norment 1999), and (2) landscape-level factors such as forest cover and configuration (review in Villard et al. 1999; Hames et al. 2001). Many authors now believe that a better understanding of landscape sensitivity could be obtained from direct behavioural study of individuals (Lima and Zollner 1996; Walters 1998; Caro 1999; Desrochers et al. 1999). Furthermore, a comparative approach exploiting interspecific differences (rather than treating them as a nuisance) is needed to move towards a general theory of avian responses to landscape structure (Desrochers 2003). To date, the behaviour of individual birds remains rarely incorporated in landscape studies (Stutchbury 1998; Bélisle et al. 2001; Norris and Stutchbury 2002).

One potential proximate cause of landscape sensitivity is the reluctance of individual birds to venture into inhospitable habitat (Harris and Reed 2002). Although Neotropical migrants routinely demonstrate great vagility (the physical ability to move long distances) during migration, their dispersal ability (the ability to reach and settle a territory) remains mostly unknown (Villard et al. 1995). What is at issue here is not whether birds can physically cross large gaps in the forest. Instead, the concern is about the cost that repeated encounters with open areas may have on avian occupancy patterns. For example, since vulnerability to predators is assumed to be greater in forest gaps (Schneider 1984; Lima and Dill 1990; Todd and Cowie 1990; Götmark and Post 1996), both juveniles and adult birds may be reluctant to cross open areas during their daily movements. Indeed, even 20-m forest gaps can impede avian movements (Sieving et al. 1996; Desrochers and Hannon 1997; St. Clair et al. 1998; Desrochers et al. 1999). Thus, the repeated encounter of such gaps, and detours to avoid them, may decrease birds' ability to explore during natal or breeding dispersal. Consequently, the probability of colonization of isolated forest patches may be reduced, as evidenced by a translocation experiment by Cooper and Walters (2002). Several patches or sectors of habitat could thus remain unoccupied despite their suitability and this situation could have important consequences for population viability.

We hypothesize that interspecific variations in reluctance to move across open habitat could explain observed interspecific differences in landscape sensitivity (Walters 1998; Desrochers 2003). Increasingly, differences in dispersal ability among species are being measured (Desrochers and Hannon 1997; Rail et al. 1997; St. Clair et al. 1998; Bélisle et al. 2001; Bélisle and Desrochers 2002) but these differences will be of little use to landscape ecologists unless they are related to species distribution in the landscape. To our knowledge, the relationship between dispersal ability and landscape sensitivity has seldom been measured, although Hannon and Schmiegelow (2002) attempted to relate avian abundance with propensity to cross gaps within an industrial landscape. However, in that study, the methodology used to measure the dispersal ability of birds was not constant amongst species.

Since the effects of habitat fragmentation for a given species can differ with perturbation types (Hansen and Urban 1992; Thompson 1993) and with geographical region (Tewksbury et al. 1998), it is necessary to measure landscape sensitivity and movement constraints in a single system. Here, we quantified patterns of occurrence of breeding bird assemblages along a fragmentation gradient in southern Québec and used behavioural trials to measure the reluctance of birds to cross gaps in the canopy. We tested whether landscape sensitivity is correlated to movement inhibition at small spatial scales. We predicted that the species most reluctant to cross open habitat will exhibit the most sensitivity to forest loss and associated fragmentation.

METHODS

Study area

The study area was located in an agricultural landscape within 50 km of Québec City (46° 45’ N, 71° 20’ O), Québec, Canada (Fig. 1). Within the study area, remaining forest patches consisted of mixed-tolerant hardwood and were sharply delimited by either agricultural fields or roads. Dominant deciduous species included red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), and sugar maple (*A. saccharum*), whereas balsam fir (*Abies balsamea*) and red spruce (*Picea rubra*) were the coniferous species most frequently encountered. Most forest patches were connected to each other by forested strips of varying width (5->100 m). Accordingly, true fragments were rare.

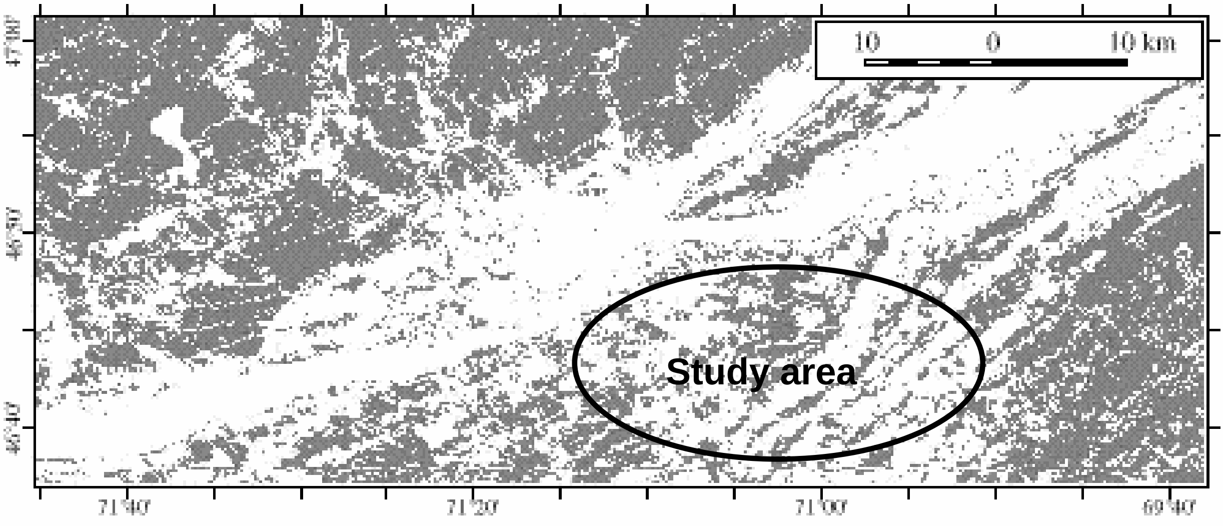

Figure 1. Layout of mature forest (grey areas) over a classified satellite image taken in 1993-1994. Québec City (46° 45’ N, 71° 20’ O), Québec, Canada, is located at the center of the map.

Landscape use

We surveyed 102 point count stations twice between 30 May and 29 June 2000. The point count stations were located at least 250 m apart and were at least 50 m from an edge. All individuals seen or heard within a 50 m radius were noted. Surveys each lasted 10 min and were conducted between 30 min before sunrise and 1000 EST, in mornings when bird detection was not impeded by wind or rain. A cumulative survey time of twenty minutes provides adequate characterization of avian assemblages in hardwood stands (Drapeau et al. 1999). We only surveyed birds in 2000, and we assume that population trends did not change in 2001 since recent work has shown that avian sensitivity to landscape structure is consistent among years for a given location (Desrochers, unpubl. data). Furthermore, forest cover and composition were not altered by agricultural practices for the duration of the study.

Landscape structure

LANDSAT-TM satellite images of the study area were taken in 1993-1994 and classified into forest and non-forest habitats by the Canadian Wildlife Service (Bélanger and Grenier 1998). The reliability of the satellite images was verified with forest inventory maps and ground-truthing. We imported the satellite images into the ArcView 3.2 Geographic Information System (ESRI 1996). We described landscape structure in 500-m radius circles centered on each point count station with the Patch Analyst extension (Rempel 2000). Since most forest songbirds censused in the study area defend territories <5 ha (Gauthier and Aubry 1995), we assumed that 500-m radius circles would include landscape characteristics relevant to the perceptual range of breeding songbirds. We used total forest cover area (ha), total core area (total forest cover [ha] >50 m from edge), and the ratio between the length of forest edge and forest cover area (m/ha) to describe landscape structure. Previous studies show that these variables sometimes explain patterns of avian distribution in fragmented forests (Paton 1994; Villard et al. 1999). The use of these variables also allowed us to rank species according to their response to the overall pattern of fragmentation. Fragment size or isolation was not used since our study area corresponded to "shredded" forests (Forman and Godron 1986) and true fragments were rare.

Avian movements

Between 24 July and 4 September 2000 and between 16 August and 15 September 2001, we conducted 313 and 251 playback trials, respectively. Before late July, territorial boundaries may have provided a behavioural impediment to movements. In each trial, we used playbacks of mobbing calls of black-capped chickadee (*Poecile atricapillus*) and red-breasted nuthatch (*Sitta canadensis*) to incite birds to cross either continuous forests or road gaps. The trials were conducted between sunrise and 1000 EST on days without rain or strong winds. The trials were usually performed along rural roads and were separated by at least 200 m. The playback approach has several advantages including the control of birds' destination and motivation in different contexts (Desrochers and Hannon 1997) and the possibility of attracting a large number of bird species (Hurd 1996; Gunn et al. 2000). Furthermore, even though birds could usually circumvent large gaps in our study area, playback experiments allow us to measure the *relative* tendency of species to avoid gaps in the canopy. Each day, we performed both treatments (forest and gaps) to avoid the confounding effect of the advancing season. Playbacks were broadcasted from a 5-W amplifier, with volume near or at the maximum level so that the stimulus sounded natural to the human ear. During the trials, 1-3 observers were stationed 10 to 20 m on either side of the amplifier. Preliminary trials with playbacks have shown that most passerines seem undeterred by the presence of observers, and readily respond to the playbacks although observers may be conspicuous and <5 m from the amplifier (Bourque, pers. obs.). We were concerned that individuals of other species might influence gap-crossing propensity of an individual. However, the black-capped chickadee, which was the species most responsive to playbacks, did not influence the response of heterospecifics during the simulated mobbing event (Bourque and Aznar submitted).

The gap (experimental) treatment consisted of inciting birds to cross a rural road separating mature forest stands. During the forest (control) treatment, birds were attracted through continuous forest along straight woodland edges. Since most rural roads in our study area had a width of 20 m (mean ± SD = 19.3 ± 5.0 m), we strived to duplicate that distance during the forest treatment. Also, previous studies have shown that 20-m gaps are sufficient to impede bird movements (Sieving et al. 1996; Desrochers and Hannon 1997; St. Clair et al. 1998; Desrochers et al. 1999). In both treatments, birds were first attracted briefly to a woodland edge with a mobbing playback. This allowed us to filter out individuals that do not respond readily to mobbing. In each trial, responsive individuals were then attracted to a second location, separated from the edge by either a forest road or continuous forest. We measured the time birds took to travel the distance from the first to the second location with a time limit of 5 min. A crossing was recorded when birds approached within 5 m of the amplifier at the second location. In cases where several conspecifics were attracted during an experiment, we recorded the response of only the first attracted individual. Conspecifics likely did not consist of members from family groups, since we never observed begging or feeding behaviour from these individuals. During the gap treatment, in instances where a bird crossed the road several times, only the time of first crossing was recorded. After each trial, the distance between the first and second location was measured with a laser rangefinder.

Statistical analyses

For the point count data, we classified a species as present when it was detected on at least one of the two visits. To improve statistical independence between point counts, we excluded species with territories possibly overlapping several point count stations, like corvids or fringillids. Furthermore, we excluded forest species that are difficult to detect with the point count method, such as raptors, hummingbirds, and grouse. Finally, to be included in the analyses, species had to be present in both treatments of the avian movement experiment. Following these criteria, ten species remained for analysis (Table 1).

Our first aim was not to correlate pattern of species occurrence with specific variables associated with landscape structure but rather to measure species' response to the overall pattern of forest cover and fragmentation in our study area. We thus used principal component analysis to reduce the number of variables describing landscape structure with the SPSS version 10 (1999) software. Total forest cover area, total core area, and the ratio between the length of forest edge and forest cover area were strongly correlated ($|\text{Pearson's } R| > 0.826$; $p < 0.001$). The first component accounted for 92.9% of the variation and represented an increase in total forest cover area (loading = 0.964) and in total core area (loading = 0.988), and a decrease in the ratio between the length of forest edge and forest cover area (loading = -0.940). Remaining statistical procedures were computed on the Statistical Analysis System, version 8 (SAS Institute Inc. 1999). For all species combined, we calculated a logistic regression with occurrence as the response variable and with the first component, species, and the interaction between species and the first component as the independent variables. This was done to ensure that species differed significantly in their response, which would warrant further investigation. For each species, we then conducted a second logistic regression to measure sensitivity to landscape structure. In this analysis, occurrence was the response variable and the first component was the independent variable. For each species, we used two indices of sensitivity to landscape structure : (1) the maximum likelihood estimates of the slope parameter divided by its standard error, and (2) odds ratio. For each species, we divided the maximum likelihood estimate by its standard error because subsequent analyses did not account for interspecies variance. With this standardization, each species had the same weight and even a species with a disproportionately small sample size (and a high variance) could not drive the relationship.

The ranking of our species may have been closely linked to the type of analyses that were used. For example, including different variables of landscape structure may have changed significantly a species' index of landscape sensitivity. For each species, we tested for this potential effect by conducting an additional logistic regression to measure occurrence in relation only to total forest cover area. Two species (black-capped chickadee and black-throated blue warbler [*Dendroica caerulescens*]) with very similar response in the analyses using the first component (Table 1) were interchanged in this new analysis. Otherwise, ranking in species response remained unchanged. Since results were similar with both logistic regressions, we present hereafter only the response to landscape structure calculated with the first principal component.

Our second aim was to obtain an index of bird reluctance to cross open habitat. Time taken to respond to playback was analyzed with proportional hazards model of Cox (1972;1975). Again, we first analyzed the data for all species combined. Afterward, for each species, we conducted a second analysis with time taken to respond as the response variable with treatment (either forest or gap), and distance between either the location of the two recordings or the gaps in forest cover as the independent variables. The effect of distance was not statistically significant, except for the black-throated green warbler (*Dendroica virens*), chestnut-sided warbler (*D. pensylvanica*), and magnolia warbler (*D. magnolia*). However, there was no correlation between treatment and distance for any of the three species ($p >$ 0.30). We used two indices of bird's reluctance to cross gaps in the forest cover: (1) the parameter estimate of the treatment effect divided by its standard error, and (2) odds ratio. Positive parameter estimates indicated that birds took less time to respond to playbacks within the forest treatment than within the gap treatment.

We used the comparative phylogenetic method (Sanford et al. 2002) to quantify the relationship between the index of landscape sensitivity and the index of birds' reluctance to cross gaps. Closely related species may share traits or adaptations through common ancestry. This creates a problem of dependence among species when using traditional correlation or regression analyses. This non-independence can be resolved by computing statistically independent contrasts for each variable (Felseinstein 1985). Each contrast represents differences between traits at a node of the phylogenetic tree. In this study, phylogeny was based on the most recent classification of North American birds (American Ornithologists' Union 1998). Following Felseinstein's method, we standardized the contrasts by the square root of their branch lengths. Since lengths were not available for all species (Sibley and Ahlquist 1990), we standardized the contrasts using three estimations of branch lengths. First, we used equal branch lengths. Second, we calculated branch lengths following Grafen (1989). Finally, branch lengths were inferred from the phylogeny of Sibley and Ahlquist (1990). Branch length diagnostics (Garland et al. 1992) indicated that the Sibley and Ahlquist (1990) option was inadequate. From this result, we performed each of the remaining analyses two times, one for each remaining option. The standardized contrasts were regressed through the origin (justification in Garland et al. 1992) and residuals were checked for normality. Furthermore, the indices of landscape sensitivity and of bird's reluctance to cross gaps were randomized 4999 times (Manly 1997). From each randomization, we derived new standardized contrasts and calculated a new regression slope. The 4999 calculated slopes were compared to the observed regression slope in order to calculate the probability of occurrence of the actual data.

RESULTS

Within the 500-m radius circles (78.54 ha) centered on point count stations, forest cover varied between 6.87 and 66.06 ha (mean ± SD = 37.02 ± 14.03 ha), while total core area covered between 1.31 and 46.25 ha of the landscapes (20.89 ± 10.78 ha). Furthermore, the ratio between the length of forest edge and forest cover area varied between 37.79 and 274.76 m/ha (123.97 ± 52.89 m/ha).

We used either the parameter estimates or the odds ratio to measure landscape sensitivity and reluctance to cross gaps. The results were similar independently of the method that was used. We thus report hereafter only the results calculated with the parameter estimates. Species had markedly different responses to landscape structure ($X^2 = 25.48$, df = 9, $p = 0.003$). However, of the ten species tested, only two responded significantly to landscape structure: American redstart (*Setophaga ruticilla*) was significantly more abundant in deforested landscapes while ovenbird (*Seiurus aurocapilla*) was associated to highly forested landscapes (Table 1; Fig. 2). There was also a strong tendency for the black-throated green warbler to occur less often in deforested landscapes (Table 1).

In 2000 and 2001 combined, 1004 individuals of 44 species were attracted to the mobbing trials. Most (eight out of ten) species retained for further analysis had a non-significant tendency to respond more readily to mobbing in the forest than across gaps (Table 2; Fig. 2). However, response to mobbing playbacks differed significantly between forests and gaps only for the magnolia warbler and the red-eyed vireo (*Vireo olivaceus*; Table 2). Again, species differed significantly in their response to playback ($X^2 = 50.78$, df = 9, $p < 0.001$).

Although interspecific variability was high in both landscape sensitivity and reluctance to cross gaps, there was no significant relationship between landscape sensitivity and reluctance to cross gaps in the forest cover, even after correcting for phylogenetic relatedness. This result held independently of the branch length estimation used ($p > 0.50$).

Given that we accept the null hypothesis (no relationship), we measured the power of our analyses for a range of effect sizes (Fig. 3). For each effect size, we simulated 5000 regressions through the origin (as used with the real dataset). The contrasts for these simulated datasets were standardized with branch lengths calculated following Grafen (1989). Moreover, the simulated contrasts were calculated from randomly generated data with the same characteristics as our observed data (i.e. parameter estimates and standard errors). The observed effect size of our experiment was low (0.11) and consequently, the associated statistical power was low (37%). However, should the real effect be double that estimated, statistical power would be approximately 80% (Fig. 3). There was almost no change in power when we simulated a doubled sample size for each species (Fig. 3).

Table 1. Species are organized from species avoiding well-forested landscapes to those associated to well-forested landscapes, as indicated by maximum likelihood estimates from logistic regression. Data were collected using point count stations in 2000 within 50 km of Québec City (46° 45' N, 71° 20' O), Québec, Canada.

Species	df	Maximum Likelihood Estimates	SE	X^2	p
American Redstart *Setophaga ruticilla*	1	-0.64	0.24	7.42	0.006
Chestnut-sided Warbler *Dendroica pensylvanica*	1	-0.24	0.27	0.78	0.38
Magnolia Warbler *Dendroica magnolia*	1	-0.20	0.30	0.46	0.50
Blackburnian Warbler *Dendroica fusca*	1	-0.11	0.25	0.19	0.66
Red-eyed Vireo *Vireo olivaceus*	1	-0.04	0.28	0.02	0.88
Black-capped Chickadee *Poecile atricapilla*	1	0.15	0.22	0.45	0.50
Black-throated Blue Warbler *Dendroica caerulescens*	1	0.16	0.20	0.62	0.43
Black and White Warbler *Mniotilta varia*	1	0.32	0.25	1.62	0.20
Black-throated Green Warbler *Dendroica virens*	1	0.40	0.21	3.60	0.06
Ovenbird *Seiurus aurocapillus*	1	0.83	0.24	11.75	< 0.001

Table 2. Species are organized from most reluctant to cross gaps in the forest cover to least reluctant, as indicated from the time taken to respond to mobbing playbacks. Time taken to respond was analyzed with proportional hazards model of Cox. During the post-breeding

periods of 2000 and 2001, we conducted 313 and 251 behavioural trials, respectively. The trials were performed within 50 km of Québec City (46° 45’ N, 71° 20’ O), Québec, Canada.

Species	*n*	df	X^2	Parameter estimate	Standard error	p
Red-eyed Vireo *Vireo olivaceus*	122	1	7.83	0.68	0.24	0.005
Magnolia Warbler *Dendroica magnolia*	61	1	4.34	1.04	0.50	0.04
Chestnut-sided Warbler *Dendroica pensylvanica*	27	1	2.32	1.06	0.70	0.13
Ovenbird *Seiurus aurocapillus*	12	1	1.88	1.75	1.28	0.17
Black and White Warbler *Mniotilta varia*	49	1	0.91	0.42	0.44	0.34
Black-capped Chickadee *Poecile atricapillus*	225	1	0.78	0.13	0.14	0.38
Blackburnian Warbler *Dendroica fusca*	23	1	0.47	0.47	0.68	0.49
Black-throated Blue Warbler *Dendroica caerulescens*	31	1	0.16	0.24	0.59	0.68
American Redstart *Setophaga ruticilla*	33	1	0.004	-0.03	0.52	0.95
Black-throated Green Warbler *Dendroica virens*	107	1	0.50	-0.22	0.31	0.48

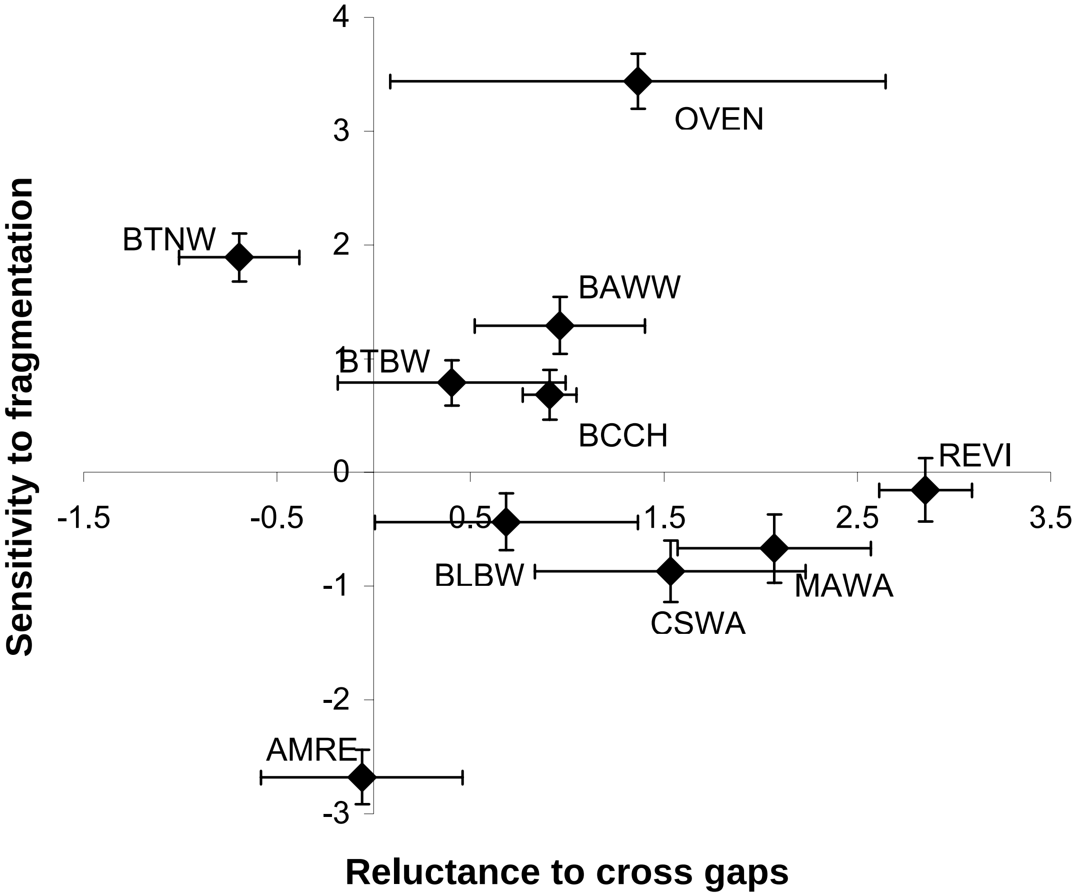

Figure 2. Indices of sensitivity to fragmentation (probability of occurrence in relation to forest structure) and of reluctance to cross gaps in the forest cover (time taken to respond to mobbing playbacks in gaps vs. forested stands) of ten forest birds, within 50 km of Québec City (46° 45’ N, 71° 20’ O), Québec, Canada. AMRE = American redstart; BAWW = black-and-white warbler; BCCH = black-capped chickadee; BLBW = blackburnian warbler; BTBW = black-throated blue warbler; BTNW = black-throated green warbler; CSWA = chestnut-sided warbler; MAWA = magnolia warbler; OVEN = ovenbird; REVI = red-eyed vireo.

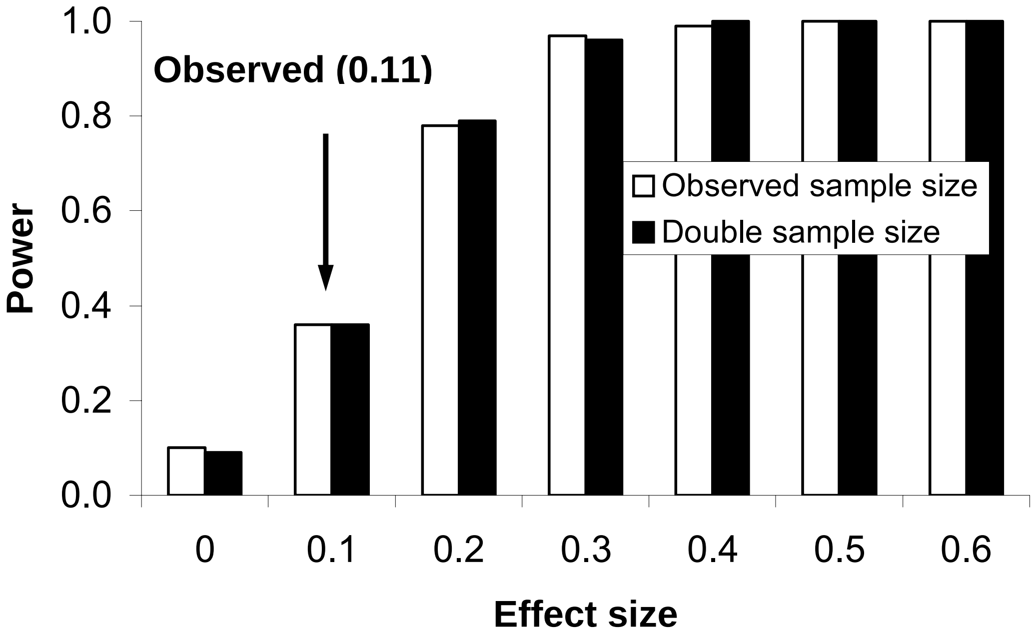

Figure 3. Power of simulated 5000 regressions through the origin. The contrasts for these simulations were randomly generated from data with the same characteristics as the observed data (i.e. parameter estimates and standard errors). The contrasts were standardized with branch lengths calculated following Grafen (1989).

DISCUSSION

We measured small-scale movement constraints of ten species within forest cover and gaps. These constraints were not related to landscape sensitivity for the species tested. This suggests that processes other than movement impediments are the driving force behind landscape sensitivity in these forest birds. For example, Lichstein et al. (2002) recently suggested that local habitat suitability likely drives the abundance of many Neotropical migrants in given parts of landscapes.

Our conclusions might have been different if more species had been studied. In our study area, however, all available species were included in our experiments. Additionally, species differed significantly in their response, which provides a first assessment of the relationship between gap-crossing behaviour and landscape use. While gap-crossing abilities apparently have little explanatory power for interspecific differences in landscape sensitivity, they may explain landscape sensitivity in some of the species considered. For example, the ovenbird was both reluctant to cross gaps in the forest cover and sensitive to landscape structure. Furthermore, some forest songbirds may associate open areas with increased energetic costs (Matthysen and Currie 1996; Hinsley 2000; Norris and Stutchbury 2001), which could reduce the probability of colonization of isolated forest patches.

In previous experiments (Desrochers and Hannon 1997; St. Clair et al. 1998; Desrochers et al. 2002), either the Red-eyed Vireo or the Black-capped Chickadee were more reluctant to respond to mobbing in open areas than in forest treatments. For the Red-eyed Vireo, our results thus concur with these previous studies. However, our result for the Black-capped Chickadee was not statistically significant. The explanation for this non-significant result may lie in the fact that we analyzed our data with proportional hazards models of Cox rather than logistic regressions. The models we used take into account the trials in which the birds did not respond in the time allowed. For most of the other species that we studied, response to mobbing playbacks was non significant between forests and gaps. However, for comparison purposes, we considered that the relative ranking of species was more important than statistical significance.

We made several assumptions during the trials and subsequent analyses of the data. First, we assumed that movement decisions made during the post-fledging period are indicative of decisions made during the period when birds investigate potential breeding territories. Accordingly, the presence of movement barriers during the post-fledging period would make fragmented forests costly to explore and result in landscape sensitivity.

Observations from several studies have suggested that birds do indeed prospect during the post-fledging period (Brewer and Harrison 1975; Adams and Brewer 1981; Morton 1992; Baker 1993). Additionally, radio-tagged juvenile wood thrush (*Hylocichla mustelina*) made extensive exploratory movements from their dispersal sites during the post-fledging period (Vega Rivera et al. 1998). Second, we assumed that response to playback did not differ according to sex. During the post-fledging period, immature males of many species closely resemble adult females, which greatly reduces the number of individuals that could be classified in the field. When sample size was sufficient ($n \geq 10$ of each sex), there was no significant effect of sex on the probability of response ($p > 0.15$ for black-throated green warbler and black-throated blue warbler). Third, we presumed that bird's response to mobbing would not change between forest cover and gaps. This assumption has been addressed recently and was supported experimentally for the black-capped chickadee and the red-eyed vireo (Desrochers et al. 2002). Finally, we assumed that our gap-crossing index would be sufficient to evaluate habitat selection at large spatial scales. This assumption stemmed from previous research that suggested that the reluctance of birds to cross small gaps could help explain avian occupancy patterns at the landscape scale (Desrochers et al. 1999). But movement constraints were not related to landscape sensitivity for the species that we tested. However, investigations of movement constraints at greater spatial scales may better explain landscape occupancy patterns of forest bird species. It is doubtful whether mobbing playbacks could be used to study avian movements on large scales (i.e. across gaps exceeding 50 m). Rather, this could be achieved by temporarily translocating territorial individuals and measuring their return trajectories with telemetry (Desrochers et al. 1999).

Within a landscape managed for timber, Hannon and Schmiegelow (2002) have tried recently to relate the abundance of 11 avian species and their propensity to cross gaps. Although the question addressed resembled ours, their methodology differed in that they often relied on habitat preferences to infer gap-crossing behaviour. For example, they assumed that habitat generalists should cross gaps easily. However, our data suggests that some species often classified as habitat generalists may find gap-crossing difficult. In fact, the red-eyed vireo is usually classified as interior/edge or generalist (Freemark and Collins 1992; Drapeau et al. 2000), while the magnolia warbler is mostly associated with forest edges or second-growth stands (Hall 1994; Drapeau et al. 2000). Both species were more willing to respond to mobbing in forests than in gaps. Our results thus suggest that the contribution of movement constraints to the occupancy pattern of these species may be minimal. Based on our observations, we also caution researchers not to infer constraints on dispersal from pattern of landscape occupancy alone.

During the last fifteen years, considerable efforts have been deployed to document landscape sensitivity in birds (review in Villard et al. 1999; Donovan and Flather 2002; Schmiegelow and Mönkkönen 2002). Even though landscape sensitivity has been identified in numerous species, the underlying mechanisms pertaining to that phenomenon remain elusive. Earlier authors have suggested that a greater understanding of movement constraints in birds might be a promising avenue (Lima and Zollner 1996; review in Desrochers et al. 1999). From a conservation standpoint, information on how individuals move in the landscape could lead to additional benefits, such as a more efficient planning of corridors (Haas 1995; Lima and Zollner 1996; Brooker et al. 1999). Such information could also allow comparisons between the permeability of different habitat types (Stamps et al. 1987; Sieving et al. 1996; Desrochers and Hannon 1997). Furthermore, there are two population models that may particularly benefit from information on the decision rules of moving individuals. The first model assumes that there may be populations that have negative population growth (sinks) and that only exist due to dispersal from source populations (Pulliam 1988). The second population model assumes that individual populations may be part of larger networks called metapopulations (Hanski 1998), in which long-term persistence may depend on dispersal (Harrison et al. 1988; Harrison 1994). Both source-sink and metapopulation models often assume realistically that dispersal is distance dependent, but continue to rely on arbitrary dispersal parameters (e. g. Moilanen and Hanski 1995; Hess 1996; Hokit et al. 2001; Ricketts 2001; South and Kenward 2001). Actual data on movement may improve the effectiveness of these models (Bélisle and Desrochers 2002). Finally, although our prediction was not supported, our index of reluctance to cross gaps remained constant throughout two years of data gathering. Thus, our approach could be transported to other, more fragmented forests and be used to provide further evidence for or against the relative contribution of movement constraints to the distribution of landscape sensitive species.

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Chapitre 2

Do mobbing calls affect the perception of predation risk by forest birds?

Desrochers[1], A., M. Bélisle[2], et Bourque[1], J. 2002. **Do mobbing calls affect the perception of predation risk by forest birds?** *Animal Behaviour 64: 709-714.* [1]Centre de recherche en biologie forestière, Pavillon Abitibi-Price, Université Laval, Québec, Qc, G1K 7P4, Canada. [2]Département de biologie, Université de Sherbrooke, Sherbrooke, Qc, J1K 2R1, Canada. *Ce chapitre est le fruit d'une collaboration entre la candidate, Marc Bélisle (candidat au doctorat à l'époque) et André Desrochers. Marc Bélisle fut responsable de la récolte des données de la section* Chickadee experiment *de ce chapitre et de la réalisation des analyses statistiques. La candidate fut responsable de la quête des données de la section* Vireo experiment *de ce chapitre. André Desrochers a participé à l'élaboration de l'idée de base de ce chapitre, a coordonné la rédaction du manuscrit et a rédigé la première version.*

Résumé

Les cris de houspillage indiquent généralement la présence d'un prédateur. Nous avons réalisé deux expériences de terrain afin de déterminer si l'exposition à des cris de houspillage provoquent des changements dans la perception du risque chez les oiseaux forestiers, telle que mesurée par la tendance des oiseaux à éviter les milieux ouverts. Dans la première expérience, nous avons testé la prédiction suivante : en hiver, les mésanges à tête noire (*Poecile atricapilla*) iront chercher de la nourriture à une mangeoire en milieu ouvert moins souvent lors d'un événement de houspillage que lors d'une situation témoin. Lors des évènements de houspillage, les taux de visite aux mangeoires ont diminué en fonction de la distance par rapport aux lisières de forêt (0-10 m). La présence de houspillage a augmenté le taux de visite global aux mangeoires, mais a diminué le taux de visite aux mangeoires placées à 10 m des lisières de forêt. Cependant, lorsqu'un faucon émerillon (*Falco columbarius*) était placé près d'une mangeoire, les mésanges visitaient rarement la mangeoire, indépendamment de la distance à la lisière de forêt. Dans la deuxième expérience, nous avons prédit que, en saison de nidification, les mâles viréo aux yeux rouges (*Vireo olivaceus*) seraient moins attirés par le chant d'un mâle conspécifique après un événement de houspillage qu'après un stimulus auditif 'neutre' de chant de mésange à tête noire. Nous avons également prédit que cet effet serait plus marqué lorsque les viréos doivent traverser un milieu ouvert. Les viréos traversaient autant les milieux ouverts après le houspillage qu'après le stimulus neutre. Par contre, les viréos répondaient plus souvent à un chant conspécifique venant du couvert forestier qu'à un chant venant de l'autre côté d'un milieu ouvert. Nos résultats suggèrent que, sous couvert forestier, les oiseaux forestiers perçoivent le risque d'un évènement de houspillage surtout en fonction de la distance à la cause du houspillage. Il s'ensuit qu'un équilibre entre les risques et les bénéfices pourrait exister chez les oiseaux qui houspillent, à moins que ces oiseaux ne soient loin du couvert forestier et/ou très près (< 5 m) d'un prédateur.

Abstract

We report the results of two field experiments assessing whether exposure to mobbing calls, which usually indicates the presence of a predator, elicits changes in risk perception as measured by the willingness of forest birds to enter or cross gaps in forest cover. In the first experiment, we tested the prediction that wintering black-capped chickadees (*Poecile atricapilla*) will travel less in open areas to seek food from a feeder during a simulated mobbing event, than they will under control conditions. Visitation rates to feeders decreased at increasing distances from forest edges (0-10 m) when mobbing calls were played. Mobbing calls increased the overall visitation rate to feeders, but lowered the rate of visits to feeders located at 10 m from forest edges. By contrast, when a stuffed merlin (*Falco columbarius*) was placed near the feeder, chickadees rarely visited the feeder, regardless of distance to forest edge. In the second experiment, we tested the prediction that breeding male red-eyed vireos (*Vireo olivaceus*) will be less attracted to the song of a nearby red-eyed vireo after a playback of a mobbing event than after a "neutral" sound stimulus, especially if they have to cross an open area. Vireos were as willing to cross a gap in forest cover following exposure to mobbing calls than otherwise, although they responded more frequently to conspecific song under forest cover than across gaps. Our results suggest that forest birds under cover assess the risk of a mobbing situation largely on the distance to the cause of mobbing. It follows that a trade-off between risk and reward may not occur with mobbing birds, unless far outside forest cover and/or at very close range (< 5 m) to a predator.

INTRODUCTION

Birds often use mobbing behaviour, mostly when they discover stationary predators (Curio 1978; Curio et al. 1978). The resulting scene often attracts mixed-species groups, whose individuals may join the mobbing. Although mobbing is a widespread behaviour in birds (Ficken & Popp 1996; Hurd 1996), no consensus has been achieved on its adaptive or ecological significance. It is often assumed that mobbing impairs the efficacy of predators, for example by confusing them or making them leave the area (reviewed by Curio 1978; Pettifor 1990; McLean & Rhodes 1991; Flasskamp 1994; Pavey & Smyth 1998). Discriminating among potential, proximate functions that drive mobbing behaviour is difficult because several functions can operate simultaneously while achieving the same apparent result.

Birds mobbing a predator tend to be highly conspicuous (Curio & Regelmann 1985; Ficken & Popp 1996), in sharp contrast to birds under immediate risk (e.g., nearby raptor in flight), which usually stop moving altogether and vocalise relatively little. Thus, birds may perceive mobbing as a less risky situation than most encounters with hunting predators. In fact, a stationary predator may represent an opportunity for mobbers to direct an honest signal (ability to withstand increased risk) to both the predator and to conspecifics, in a way consistent with the handicap principle (Zahavi 1975; Grafen 1990; Caro 1995). The latter hypothesis is particularly plausible for cases in which the immediate threat is questionable, such as diurnal songbirds mobbing a strictly nocturnal owl (Harvey & Greenwood 1978). Nevertheless, predators do sometimes catch mobbers (reviewed by Curio & Regelmann 1985; McLean & Rhodes 1991; Pavey & Smyth 1998), and may elicit prudent behaviour at close range (Curio & Regelmann 1985). It thus remains at issue to what extent and under what circumstances birds consider mobbing a risky situation.

In addition to behavioural and evolutionary ecologists, conservation biologists have recently become interested in the significance of mobbing, for this behaviour is increasingly used to lure birds in experiments pertaining to landscape-level analyses of avian behaviour (e.g., Desrochers et al. 1999; Gunn et al. 2000). Yet, for the reasons stated above, the use of mobbing playbacks as attractors in experiments may generate bias depending on how prudently birds act when exposed to mobbing as opposed to other situations.

Thus, whether the emphasis is adaptive significance or movement analysis, one key element to our understanding of mobbing is knowing when and to what extent birds consider mobbing a risky situation. Here we report the results of two field experiments, one with wintering black-capped chickadees (*Poecile atricapilla*), the other with breeding male red-eyed vireos (*Vireo olivaceus*). Each experiment was designed to compare whether exposure to mobbing calls elicited changes in risk perception as measured by the willingness of birds to enter or cross gaps in forest cover where predation risk is assumed to be greater (Schneider 1984; Todd & Cowie 1990; Götmark & Post 1996). Each experiment thus assumes that mobbing calls provide information about the presence of a predator.

METHODS

We conducted both experiments in agricultural and urban landscapes within 75 km of Québec City (46° 45’ N, 71° 20’ W), Québec, Canada. All forest edges were sharply delimited either by roadsides, agricultural fields, or urban areas. Forests were dominated by sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*) and balsam fir (*Abies balsamea*).

Chickadee experiment

Wintering black-capped chickadees forage in flocks of up to 12 individuals within a home range of about 20 ha, and are often accompanied by individuals from other resident bird species (Dolby & Grubb 1999; Desrochers & Fortin 2000). Chickadees exhibit prudence towards open areas (Desrochers & Hannon 1997; St. Clair et al. 1998). If chickadees respond to mobbing calls by additional prudence, we predict that they will travel less in open areas to seek food from a feeder during a mobbing event than they will under control conditions.

We placed bird feeders near forest edges in 25 locations separated by at least 2 km. Each feeder was filled with sunflower seeds and placed 1.5 m above ground on a post in the forest, < 3 m of the forest edge. After their erection, feeders were left unattended for periods of 1-3 days to get chickadee flocks to use them. When feeder use by chickadees was confirmed, we moved the feeder and its post in the open at a randomly-assigned distance of either 0 m ($N = 9$), 6 m ($N = 8$) or 10 m ($N = 8$) from the forest edge. Feeder distances were fixed for each location. We placed a 2-m high balsam fir for cover right beside each feeder. At each site, we made two visits separated by at least 1 day. During each visit, a control (feeder only) treatment preceded one of two experimental treatments. A "Mobbing" treatment consisted of a 5-min playback of a chickadee-nuthatch (*Sitta canadensis*) mobbing scene played from a Rio® MP3 player connected to a 5-W amplifier concealed in the dense core of the sapling fir. We adjusted the volume near or at the maximum level so that the stimulus sounded natural to the human ear. The mobbing scene was recorded in December 1991, with a Dan Gibson 44 cm parabola and a Sony TCM-5000 cassette recorder, 5 m from a bird feeder 20 km northeast of Québec City. A lyophilised Eastern screech owl (*Otus asio*) was placed on the bird feeder to elicit mobbing calls during the recording session.

To further examine the response of chickadees to potential threats, we conducted a "Merlin" treatment by placing a stuffed merlin (*Falco columbarius*) at the top of the sapling fir. Merlins are occasional aerial predators in our study area in both winter and summer. Each flock was thus subjected to two experimental treatments, applied in random order, each with its own control. Each treatment was initiated with chickadees already present at the feeder. We estimated flock size and measured the number of trips made to the feeder by chickadees within a fixed, 5-min period. Note that only one chickadee could obtain seeds from the feeder at any one time. Yet, chickadees could not monopolise the feeder because they cannot handle more than one or two seeds at a time and because they usually went to a branch to crack the seeds open. We also recorded mobbing and alarm calls (the latter referred to as *high zees* by Ficken et al. 1978) made by chickadees in the vicinity of the feeder. All chickadee trials were conducted in days with no strong winds, between 0705 and 1130 hours EST, from 28 January to 3 March 1998.

We analysed the chickadee experiment as a repeated-measures design with generalised estimating equations, which constitute an extension of generalised linear models (GEE's, see Horton & Lipsitz 1999). The model was fitted using the GENMOD procedure of SAS 8.01 assuming an unstructured correlation matrix (SAS Institute Inc. 1993). Since the response variable was a number of visits to feeders, a log link function with Poisson errors was chosen. The size of the flock (log-transformed) was used as an offset variable in the model to control for its effect on visitation rates.

Vireo experiment

Breeding male red-eyed vireos sing throughout most of the day and strongly defend territories of about 0.5 ha in size (Darveau & Barrette 1995). If breeding vireos perceive mobbing calls as indicative of predation risk, they should exhibit increased prudence at least a few minutes after the exposure to mobbing calls (Hegner 1985). Thus, we predict that vireos will be more reluctant to approach a conspecific singing after a playback of a mobbing event than after a "neutral" sound stimulus. This mobbing effect should also be more pronounced if vireos have to cross an open area to get to the stimulus than if they can remain under forest cover, because of presumed increased predation risk in the open (see above).

Eighty-four territorial male red-eyed vireos, whose territories were separated by at least 100 m, were selected in the agricultural woodlots of the study area. Each vireo was subjected to one of four playback trials, played at a volume sounding natural to the human ear, from a Rio® MP3 player connected 5-W amplifier placed on the ground, oriented towards the vireo. Two recordings were used, each consisting of two parts. The first recording (mobbing) was 2 minutes of chickadee-nuthatch mobbing calls (same playback as in the chickadee experiment) followed by 4 minutes of song of a red-eyed vireo. The second recording (control) was 2 minutes of chickadee song (*fee-bee*; Ficken et al. 1978) followed by 4 minutes of red-eyed vireo song. Vireo and chickadee songs were obtained from the *Peterson Field Guide To Bird Songs (Eastern/Central)* CD and edited digitally with Sonic Foundry's *SoundForge* 5.0 software.

Thus, recordings were made such that we could measure whether the response of vireos to conspecifics was modulated by prior exposure to mobbing calls. Each recording type was used to attract vireos either through continuous forest ($N = 39$), or across a 12 – 28 m gap defined by a rural road ($N = 45$), to assess whether the response to mobbing was itself affected by having to fly outside forest cover. In each trial, the singing vireo was attracted in two steps: first, by a short (< 30 s) playback of vireo song to ascertain its initial position and willingness to respond, and second, by the experimental recording, played at 10 – 35 m from the location where the bird was first attracted. The latter distance range is less than the radius of roughly 40 m an average vireo territory has (Darveau & Barrette 1995). The distance between the vireo and the speaker at the onset of the second part of experimental recordings (i.e., red-eyed vireo song) was measured with a laser rangefinder. In each trial, vireos were classified as responding if they came to the speaker (< 5 m) during the second part of the recording. Cases in which vireos had moved to < 10 m of the speaker by the onset of the playback of vireo song were not considered in the analysis. All trials were conducted from 29 June 2000 to 29 July 2000 by a team of two observers, between 0500 and 1130 hours EST on days without rain or strong winds. The order of treatments was randomised and each treatment was performed each day to avoid the confounding effects of the evolving breeding season.

Vireo responses were analysed with a logistic regression based on a completely-randomised design, with recording type and presence of a gap as main effects. The distance of the vireo to the speaker at the onset of the vireo song in the experimental playback was entered as a covariable in the model which was fitted using the GENMOD procedure of SAS 8.01 (SAS Institute Inc. 1993).

RESULTS

Chickadee experiment

Chickadee flocks ranged in size from 2 to 12 birds (mean ± SD = 4.3 ± 2.0). With all treatments combined, flocks visited feeders at rates varying from 0 - 7.2 visits • individual^{-1} • 5-min^{-1}. During controls, averaged visitation rates were not significantly associated with averaged flock size ($r_{24} = 0.15$, $P = 0.47$). Overall, the most pronounced treatment effect was that of the merlin. When a stuffed merlin was present, chickadees only rarely went to the feeder, regardless of distance to forest edge (Fig. 1a). Furthermore, the stuffed merlin elicited mobbing and alarm calls in 60 % and 76 % of the 25 flocks, respectively. In contrast, no mobbing or alarm calls were uttered during controls.

Unlike the merlin treatment, mobbing calls did not stop chickadees from using feeders in the open (Fig. 1b). For each distance class, visitation rates to feeders were similar with and without mobbing calls. However, mobbing calls led to a negative effect of distance to edge on the visitation rates of chickadees, which was not apparent in situations without mobbing (statistical interaction in Table 1). It is noteworthy that the negative effect of distance to edge is as much the result of an increased visitation rate at the forest edge than a reduced one at 10 m from the edge. Also, even though 60 % of flocks uttered mobbing calls during mobbing playbacks, they never made alarm calls in this treatment. Again, no mobbing or alarm calls were uttered during controls.

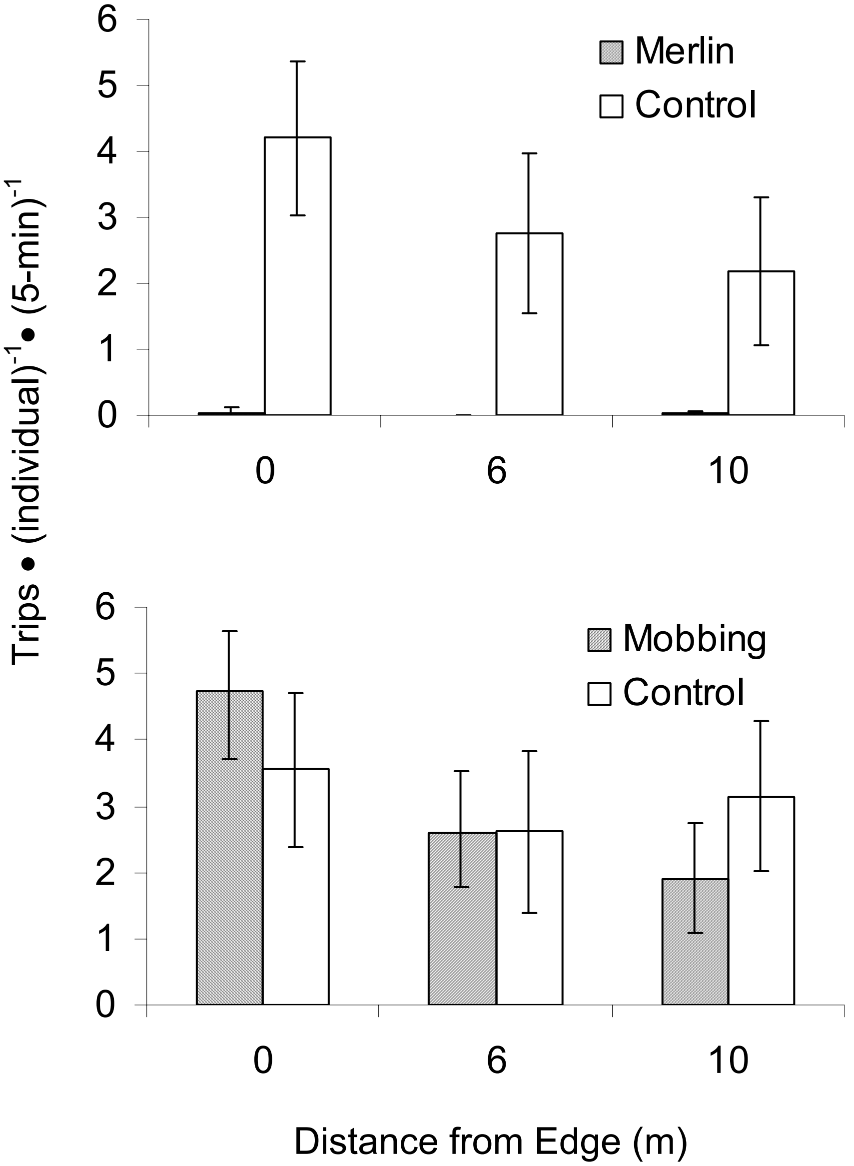

Figure 1. Visitation rates of wintering black-capped chickadees to a sunflower-seed feeder placed in the open, at three distances from the forest edge. A) in relation with the presence chickadee-nuthatch mobbing calls, B) in relation with the presence of a stuffed merlin. Vertical lines represent 95% confidence limits of means, bootstrapped from 999 resamples. Sample sizes varied from 8 – 9 flocks per bar.

Table 1. Effects of distance to forest cover and exposure to chickadee-nuthatch mobbing calls on visitation rate of wintering black-capped chickadees to sunflower-seed feeders. Parameter

estimates obtained from a generalised linear model with repeated measures ($N = 25$ locations), Poisson errors and a log link function. Estimates were offset by the log of flock size. Standard Errors were adjusted by a scale parameter.

Effect	*df*	Parameter estimate	Std Error	*z*	*P*
Distance	1	-0.106	0.021	-5.01	<0.001
Mobbing[1]	1	0.307	0.084	3.64	<0.001
Distance * Mobbing[1]	1	-0.083	0.022	-3.74	<0.001

[1] Effect relative to control (latter group used as reference category).

Vireo experiment

Vireos responded to conspecific song immediately (< 30 s) in 81 % of playbacks, with no major change in the course of the season ($r_{83} = 0.10$). Their response was more frequent under forest cover than across gaps (Table 2; Fig. 2). However, their response was not markedly affected by mobbing, irrespective of the presence of a gap in the forest canopy (main effect and interaction in Table 2). The lack of negative response to mobbing is further demonstrated by the fact that 15 trials had to be cancelled because the vireos came within 5 m of the speaker (sometimes < 1 m) *during* the 2-minute broadcast of mobbing calls, whereas no vireo approached the speaker while the chickadee song was playing. Thus, either vireos experienced no lasting effect of mobbing calls, or they did so without perceiving increased predation risk.

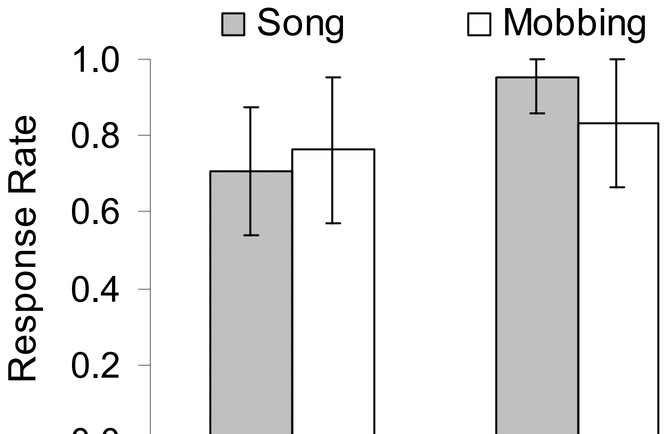

Figure 2. Response of breeding male red-eyed vireos to conspecific song playback preceded either by black-capped chickadee song (control) or by chickadee-nuthatch mobbing calls. Vertical lines represent 95% confidence limits of means, bootstrapped from 999 resamples. Sample sizes varied from 18 – 24 individuals per bar.

Table 2. Effects of a gap in forest cover and of prior exposure to chickadee-nuthatch mobbing calls on response rates of breeding male red-eyed vireos to conspecific song. Parameter estimates obtained from a generalised linear model with completely randomised design ($N = 84$ vireos), binomial errors and a logit link function. Standard Errors were adjusted by a scale parameter.

Effect	*df*	Parameter estimate	Std Error	Chi-square	*P*
Distance	1	-0.089	0.07	1.81	0.18
Gap[1]	1	-2.579	1.18	4.78	0.03
Mobbing[2]	1	-1.676	1.21	1.91	0.17
Gap * Mobbing	1	1.976	1.39	2.02	0.15

[1] Woodland used as reference category.

[2] Control (chickadee song) used as reference category.

DISCUSSION

Chickadees exhibited signs of prudence while vireos were apparently undeterred by a simulated mobbing event. Prudent behaviour associated with chickadees exposed to mobbing calls was suggested by their reduced visitation rate to feeders far (10 m) from forest cover. However, chickadees used the feeders placed 6 m into the open at equal rates with or without mobbing. Also, they uttered alarm calls and refused to leave the forest only in the presence of a perched merlin. Thus, while chickadees behaved somewhat more prudently than under normal circumstances when exposed to mobbing calls, their response was subtle compared to their response to a perched merlin, pointing to a different function of mobbing relative to alarm situations.

In a very different context, vireos showed great variability in their response to the mobbing treatment, resulting in a lack of mobbing effect despite a sizeable sample size. Nevertheless, vireos were globally as willing to cross a gap in forest cover following exposure to mobbing calls as otherwise, even though they were generally reluctant to leave forest cover, as are several other species under similar conditions (Desrochers and Hannon 1997). Results could have differed if we had used a stuffed or live owl in addition to the recording of mobbing calls, but the work of Curio & Regelmann (1985) suggests that even a live owl makes little difference in risk perception during mobbing. It is difficult to assess whether vireos were less likely to investigate a conspecific when having to cross a gap in the forest because the open area strictly marked the boundary of territories or because venturing in the open mainly resulted in a greater predation risk (Grubb & Doherty 1999; Hinsley 2000). However, the former explanation is unlikely as forest birds regularly make excursions outside their territory boundaries to investigate intruders (Falls 1981). Finally, it could be argued that vireos did not respond to mobbing simply because they assumed that the cause of mobbing (and the associated threat) was gone immediately when mobbing calls ended, followed by the song of a vireo in the same location. However, a predator on the move following mobbing would likely represent a greater risk than a mobbed, motionless predator. Additionally, several studies show that birds experience lasting responses following a short exposure to predation risk (reviewed by Hegner 1985; Lima 1985). For example, Hegner (1985) estimated that blue tits (*Parus caeruleus*) stopped moving for an average of 2.4 minutes after a mock sparrowhawk (*Accipiter nisus*) was flown over them. Analogously, Forsman et al. (1998) found that birds' spatial distribution was affected even one day after exposure to a stuffed avian predator. Vireos did not exhibit such lasting prudent response as they generally came to the speaker almost immediately after the end of mobbing calls, if they were not already there.

Costs involved with mobbing are real and documented, mostly as anecdotal observations (see references in McLean & Rhodes 1991) but sometimes more quantitatively (Pavey & Smyth 1998). Accordingly, Curio & Regelmann (1985) found that great tits (*Parus major*) mobbing a caged owl were gradually more careful as they approached it from 5 m to 1 m, based on the their flight patterns. The potential danger associated with approaching a predator at close range may explain why chickadees lowered their rate of visits to feeders located at 10 m from forest edges when exposed to mobbing calls. Indeed, chickadees often spent time apparently investigating the mobbing scene from the forest edge before flying to the exposed feeder. It remains that in nearly all flights to the feeder chickadees investigated the conifer placed in the open (besides the feeder and from which mobbing calls were emitted). Hence, the mobbing stimulus was safe enough to induce chickadees to fly out of forest cover and perch within 1 m of a hypothetical predator without previously seeing it, invariably within less than 5 minutes.

The chickadee experiment is unlikely to be representative of most mobbing situations where mobbers can keep their distances with the predator while investigating it. Prudent behaviour by mobbers in these more typical situations has been ignored or assumed, but not measured prior to this study. Our experiment with the vireos was especially designed to detect such prudent behaviour and produced results opposite from the work of Curio & Regelmann (1985). Thus, for birds under cover, whether mobbing is assessed as risky seems largely a matter of distance to the cause of mobbing, with a strong contrast between distances of < 5 m and greater distances. It follows that a trade-off between risk and reward may not occur with mobbing birds, unless far outside forest cover and/or at very close range to a predator.

Mobbing acts as a powerful attractor for a large number of bird species (Hurd 1996) and has enormous potential for field experiments designed to direct bird movements to a specific location, especially outside the breeding season, when conspecific song playback is of limited use. Recent work has relied extensively on the assumption that the birds attracted to a recording of mobbing will not act more prudently than otherwise (Desrochers & Hannon 1997; St. Clair et al. 1998; Bélisle & Desrochers 2002). Our findings support this assumption, except in cases when mobbing birds approach a predator within a few meters. Thus, the use of mobbing calls in field experiments will generally create no bias in bird movements, provided that birds remain at distances of several meters from the speaker. Although our two experiments pointed to similarities in response to mobbing in two very contrasted situations, they also provide enough differences to warrant prudence in our attempts to generalise on how much mobbing is assessed as a risky situation in birds. Future experiments intended at assessing the risk taken by mobbing birds would benefit from using a "titration approach" that translates the risk of predation into an energy currency. For instance, forest birds could be given the choice to distribute themselves between a feeder and a mobbing scene separated by different habitats (forest vs. open). Such an approach would be analogous to the one used in tests of the ideal free distribution theory (Abrahams & Dill 1989; Houston et al. 1998; see also Todd & Cowie 1990).

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Chapitre 3

Spatial aggregation of forest songbird territories and possible implications for area-sensitivity

Bourque, J., et A. Desrochers. **Spatial aggregation of forest songbird territories and possible implications for area-sensitivity.** Sera soumis à *Ecological Applications*. Centre de recherche en biologie forestière, Pavillon Abitibi-Price, Université Laval, Québec, Qc, G1K 7P4, Canada. *Ce chapitre est le fruit du travail du candidat. André Desrochers a participé à l'élaboration de l'idée de base de ce chapitre.*

Résumé

La sensibilité à la structure des forêts varie grandement entre les espèces, mais les causes de cette variation demeurent méconnues. Par contre, des études récentes montrent que les mâles de certaines espèces préfèrent installer leur territoire près de ceux de voisins conspécifiques. Les espèces requérant de grandes superficies pourraient donc être celles qui ont tendance à regrouper leurs territoires puisque les besoins spatiaux des individus seraient beaucoup plus grands que la superficie d'un seul territoire. Les objectifs de cette étude étaient (1) de quantifier la tendance à se regrouper des oiseaux forestiers territoriaux et (2) de mesurer, avec une banque de données indépendante, la relation entre la tendance à se regrouper et la sensibilité à la structure des forêts. Nous émettons la prédiction suivante: les espèces qui regroupent le plus leurs territoires seront celles associées positivement à la quantité de forêt. Après avoir controlé les patrons spatiaux de la végétation, les territoires de neuf espèces sur 14 était significativement autocorrélés à au moins une échelle spatiale. Cependant, le degré d'aggrégation spatiale des territoires ne permettait pas de prédire la répartition des espèces, quelle que soit l'échelle spatiale étudiée. Puisque 64% des espèces avaient tendance à regrouper leurs territoires, nous concluons que l'aggrégation des territoires est un phénomène commun chez les oiseaux forestiers. L'aggrégation spatiale des territoires mérite donc d'être incorporée dans de futures études sur la répartition des populations d'oiseaux forestiers.

Abstract

Habitat area requirements by forest songbirds vary greatly among species, but the causes of this variation are not well understood. High area requirements could result from advantages for certain species to establish their territories near those of conspecifics, thus resulting in spatial aggregations much larger than single territories. The objectives of this study were twofold : (1) to seek evidence for territory clusters for forest birds, and (2) to measure with an independent dataset the relationship between the tendency to occur in clusters and landscape sensitivity. We predicted that more spatially-aggregated species would respond more positively to the amount of forest in the landscape. After controlling for habitat spatial patterns, locations of singing males of nine out of 14 species were significantly clustered in at least one spatial scale. However, spatial aggregation of territories was not a good predictor of landscape occupancy patterns at any of the spatial scales that were studied. Since 64% of the species studied clustered their territories, we conclude that territorial aggregation is a common phenomenon in forest songbirds, and should be addressed in the study of avian distribution patterns.

INTRODUCTION

Forest songbird distribution is usually considered to depend mainly on forest structure and composition at different spatial scales (McGarigal and McComb 1995, Hagan et al. 1997, Schmiegelow et al. 1997, Penhollow and Stauffer 2000). However, several factors could have an additional effect on avian distribution. A few examples show that non-colonial birds will sometimes settle their territory preferably near conspecifics (Alatalo et al. 1982, Smith and Peacock 1990, Ray et al. 1991, Reed and Dobson 1993, Lima and Zollner 1996, Muller et al. 1997, Stamps 2001, Doligez et al. 2004, Ward and Schlossberg 2004). This behaviour may confer advantages in predator detection (Kenward 1978, Bildstein 1983, Stephens and Sutherland 1999, Perry and Andersen 2003) and greater opportunities in extra-pair mating (Wagner 1997, Norris and Stutchbury 2001). Alternatively, individuals may simply use the presence of conspecifics to assess habitat quality when selecting a territory (Kiester and Slatkin 1973, Smith and Peacock 1990, Reed and Dobson 1993, Stamps 1987, 1988, 1994). Loose aggregates of individual territories could thus be created within contiguous forests by this phenomenon.

Theoretically, species that prefer to settle near conspecifics could show reduced population viability in highly fragmented landscapes, since remnant forest patches may remain unoccupied if they are too small to accommodate several territories. Thus, even though sizeable forest fragments may remain in a landscape, species that tend to aggregate may experience a greater loss of habitat than species with no tendency to aggregate. Moreover, after a local extinction, lack of conspecifics could impede recolonisation of empty but otherwise suitable forest fragments if they remain unnoticed by settling individuals (Smith and Peacock 1990, Lima and Zollner 1996, Ward and Schlossberg 2004). These additive effects could result in the observed area sensitivity (lower probability of presence in small forest fragments) reported for several species in the last fifteen years (review in Villard et al. 1999). Thus, knowing which species tend to aggregate in contiguous forests could help identify species likely to be negatively affected by forest fragmentation. Species at risk could therefore be identified more readily (Fahrig and Merriam 1994, Wiens 1994).

Relatively few studies have incorporated specifically spatial structure when studying the distribution of forest birds (Brown et al. 1995; Drolet et al. 1999; Koenig 1998; 2001; Lichstein et al. 2002a). Most studies aimed to measure how species respond to their habitat by partialling out spatial components in habitat variables (Keitt et al. 2002; Dale and Fortin 2002; Lichstein et al. 2002a; 2002b). After addressing the issue of spatial autocorrelation in environmental variables, some studies still detect spatial aggregations in species distribution (Drolet et al. 1999, Lichstein et al. 2002a; 2002b). When detected, such spatial aggregations are usually treated as a statistical nuisance (e.g., Dale and Fortin 2002). However, spatial patterns at fine scales may be indicative of behavioural processes such as settlement preferences (Legendre 1993). As such, spatial aggregations at fine scales deserve to be investigated as a potentially important phenomenon.

Here, we report on the degree of aggregation of 14 forest bird species at various spatial scales (lags of 250-550 m) before and after controlling for the effects of vegetation structure. We also test whether spatially aggregated species respond most negatively to the amount of forest in the landscape. We addressed the latter prediction with species occurrence data obtained from the same study area.

METHODS

Study area

The study was conducted in 2000 and 2001 within 30 km of Québec city (46° 45’ N, 71° 20’ O), Province of Québec, Canada. The study area encompassed approximately 1200 km^2 of agricultural landscape. We selected eight 2 x 2 km plots located at least 2.5 km apart. We randomly selected four of these plots to be censused in 2000 and the remaining plots to be censused in 2001 (Fig. 1). Mature forest cover varied from 20.5% to 52.7% in each plot and the remaining land area consisted mainly of agricultural fields, roads, pastures and houses. There was a high degree of connectedness in the landscape with most forest patches being connected to each other by forested strips.The dominant deciduous tree species were Red Maple (*Acer rubrum*), Sugar Maple (*Acer saccharum*) and Yellow Birch (*Betula alleghaniensis*) while Balsam Fir (*Abies balsamea*) and Red Spruce (*Picea rubra*) were the most dominant conifers.

Avian surveys

Within each plot, ten parallel transect lines were placed systematically on a north-south axis every 200 m. From 1 June to the first week of July 2000 and 2001, each selected plot was surveyed once. Surveys took place into forested stands between 0500 and 1000 EST on days without wind or rain. We estimated the horizontal distance from the observer to every forest bird that was seen or heard within 100 m of the transects (following Bibby et al. 1992). We noted all counter-singing males in order to minimize the possibility of surveying the same individual twice. Prior to collecting data, all observers were trained in estimating the position of singing birds with a laser range-finder. A laser range-finder was used also in the field to estimate the position of likely songposts located >50 m from transect lines.

Sampling stations were established systematically every 200 m along the transect lines. We kept only the sampling stations that were located within forested stands. After the surveys, each bird detection was assigned to the nearest sampling station. Thus, at each sampling station, we had information on the occurrence of each species.

Measuring spatial autocorrelation

For each species, we used the Passage software (Rosenberg 2001) to analyze spatial autocorrelation using all sampling stations (i.e., within all woodland). The degree of spatial autocorrelation of occurrence was measured at spatial scales (distance lags) varying from 250 to 550 m with intervals of 100 m. Most songbird species defend territories < 2 ha (Ehrlich et al. 1988). Thus, we assumed that clusters of presence would occur at the chosen spatial scales. Each 100-m interval contained between 172 and 1055 pairs of sampling stations. We used Moran's *I* coefficient (Legendre and Fortin 1989) to quantify the spatial autocorrelation for each species and for each spatial scale. Moran's *I* varies between –1 and 1. For presence/absence data, negative values indicate distribution in regular arrays (e.g. caused by territorial spacing) whereas positive values indicate distribution in clusters (e.g. caused by conspecific attraction). Within each correlogram, four spatial autocorrelations were calculated.

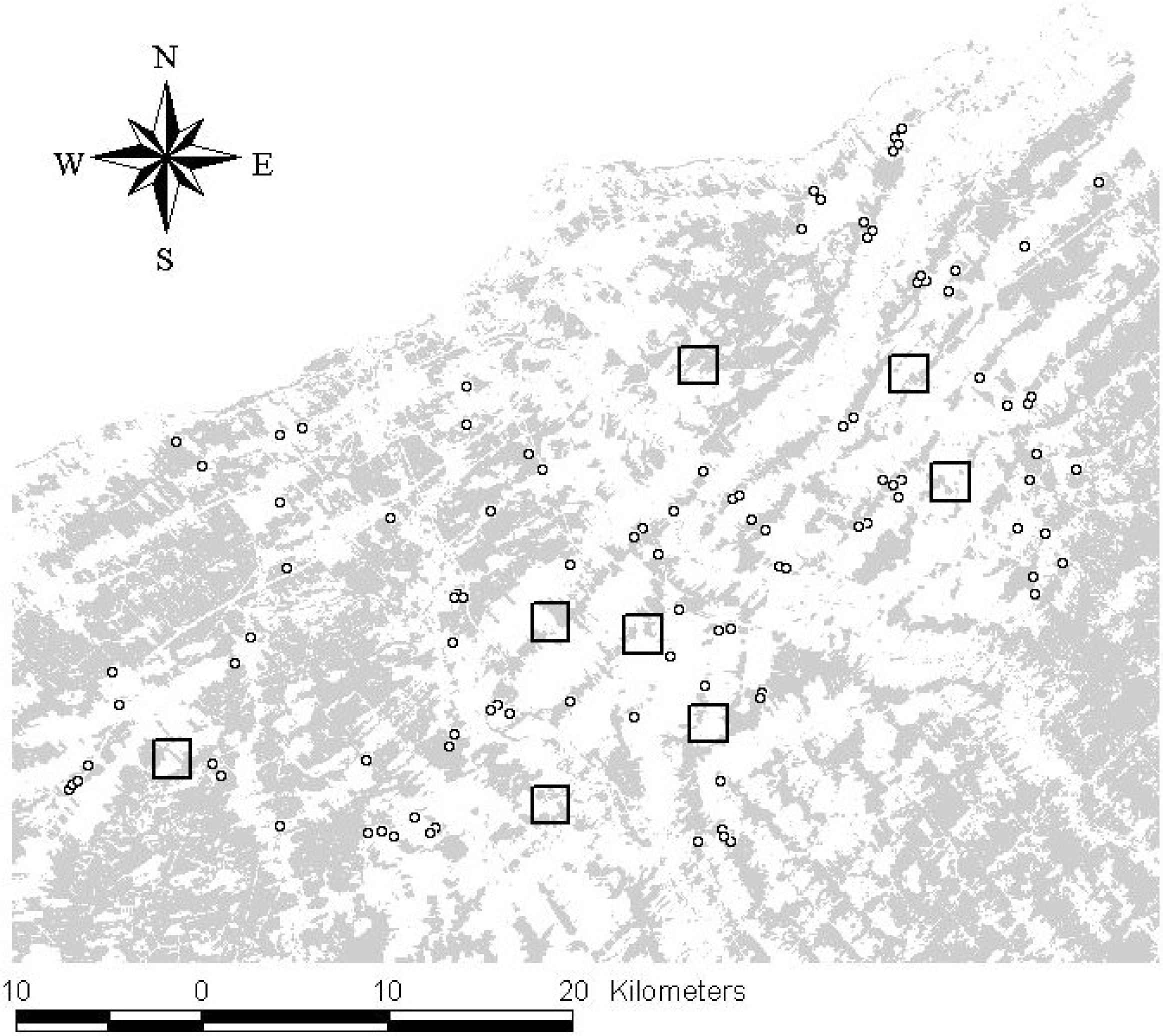

Figure 1. Layout of 102 point count stations and eight plots (2 x 2 km) over a classified satellite image. Sites were located within 50 km of Québec City (46° 45’ N, 71° 20’ O), Québec, Canada. Mature forest is represented by the grey areas while the white areas represent all other types of habitat (agricultural fields, roads, human settlements, bodies of water).

Therefore, significance of *I* was calculated with the progressive Bonferroni corrected α of 0.05/4 = 0.0125 (Legendre and Legendre 1998).

Accounting for local habitat variables

Between 31 May and 2 July 2000 and 2001, we delimited a 100-m radius circle around each sampling station and sampled three vegetation strata: canopy (> 7 m), subcanopy (2-7 m), and shrubs (0.5-2 m). Within each stratum, we visually estimated the percent cover of each of the three most common species. These variables were chosen because we considered them to reflect structural differences among stations and to be important for forest songbird habitat. These variables have also been shown to accurately predict avian assemblages in previous studies (DesGranges et al. 2001). We used principal component analysis to reduce the number of variables describing local habitat features with the SAS program, version 8 (SAS Institute Inc. 1999). The first two components accounted for 75.7% of the variation present in the data. Thus, each sampling station could be represented with the first two components of the principal component analysis. For each species, we treated the first two components as X and Y coordinates for each station and imported them into the ArcView 3.2 Geographic Information System (ESRI 1996). We calculated the 95% adaptive kernels around the sampling stations where each species occurred (Fig. 2). We considered kernels for each species as 2-dimensional representations of their potential habitat. Thus, to account for local habitat variables that may influence species distribution, for each species we considered only sampling stations inside kernels. Hence, each species had its own subset of sampling stations (i.e., those within kernels) submitted to spatial autocorrelation analysis. According to the species studied, 77.0-98.9% of the sampling stations were analysed.

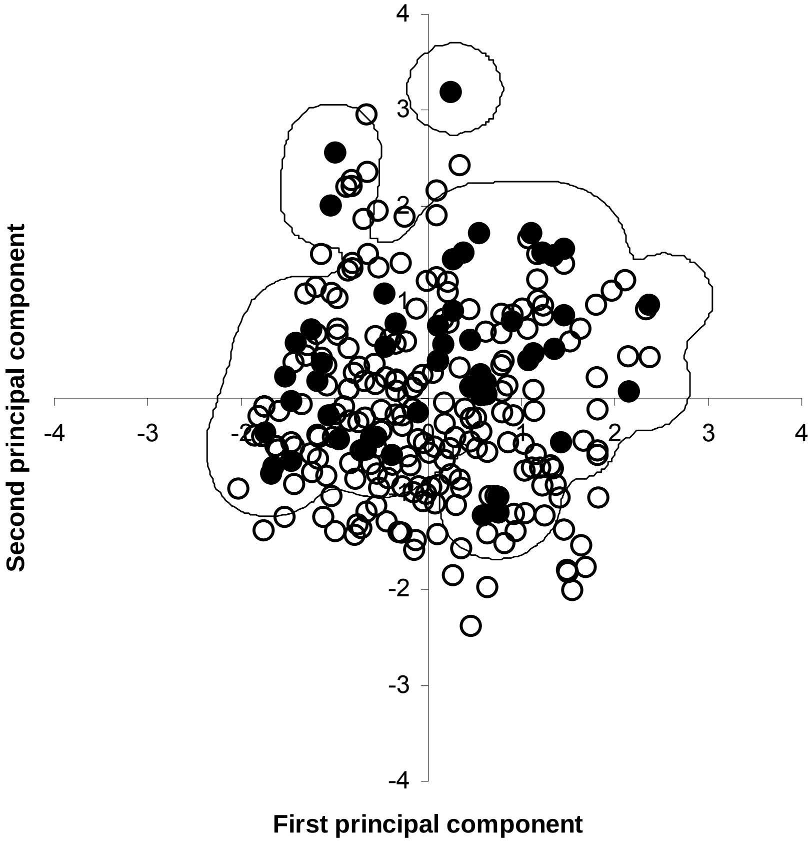

Figure 2. Adaptive kernels (95%) calculated with the occurrence data of the Magnolia Warbler (*Dendroica magnolia*). Coordinates were obtained from a principal component analysis performed on local vegetation data. Each point represents a sampling station. Open circles: species absent. Closed circles: species present. Points inside kernels were considered to contain potential habitat.

Measuring landscape use

In Chapter 1, we surveyed 102 point counts stations twice between 30 May and 29 June 2000 (Fig. 1). The point count stations were located outside of the eight plots mentioned above, were spaced at least 250 m apart, and were located > 50 m from an edge. At each point count station, we recorded all individuals seen or heard within a 100 m radius. Each survey lasted 10 min and was conducted between 30 min before sunrise and 1000 EST, in mornings without wind or rain. Additional details on bird point counts can be found in Chapter 1.

LANDSAT-TM satellite images of the study area taken in 1993-1994 were classified into forest and non-forest habitats (Bélanger and Grenier 1998). We imported the satellite images into the ArcView 3.2 Geographic Information System (ESRI 1996). We used the Patch Analyst extension (Rempel 2000) to quantify landscape composition within circles centered on each point count stations. The circles were of various radii, ranging from 250 m to 550 m, with a distance increment of 100 m. Within each radius, we measured total forest cover area (ha). Since the inclusion of configuration variables did not modify the species' response (Chapter 1), we used only forest cover area to assess landscape sensitivity. Fragment size or isolation was not used since forested areas were usually connected at the spatial scales we considered.

For each point count station, a species was considered present when it was detected in at least one of the two visits. Fourteen species were present in ≥ 10% of the stations. We considered these fourteen species to be present in sufficient number to be included in the analyses (Table 1). For each species, we used a logistic regression to measure sensitivity to landscape composition with occurrence as the response variable and with forest cover as the independent variable. We used as an index of sensitivity to landscape composition the maximum likelihood estimates of the slope parameter divided by its standard error. Again, we used the progressive Bonferroni correction (α of 0.05/4 = 0.0125; Legendre and Legendre 1998) to assess significance level.

Table 1. Probability of occurrence in relation to forest cover of 14 species, as indicated by maximum likelihood estimates from logistic regression. Data were collected using 102 point

count stations in 2000 within 50 km of Québec City (46° 45' N, 71° 20' O), Québec, Canada. Results of test: * p<0.05, ** p<0.01, *** p<0.001.

	Maximum Likelihood Estimates (SE)			
Species	250 m	350 m	450 m	550 m
Yellow-bellied sapsucker *Sphyrapicus varius*	**0.08 (0.04)***	**0.04 (0.02)***	**0.03 (0.01)***	0.02 (0.01)
Red-eyed vireo *Vireo olivaceaus*	-0.32 (0.24)	-0.15 (0.11)	-0.11 (0.07)	-0.07 (0.04)
Black-capped chickadee *Poecile atricapillus*	0.02 (0.04)	0.01 (0.02)	0.01 (0.01)	<0.01 (0.01)
Veery *Catharus fuscescens*	-0.04 (0.04)	-0.02 (0.02)	-0.01 (0.01)	-0.01 (0.01)
Hermit thrush *Catharus guttatus*	0.01 (0.04)	<-0.01 (0.02)	<-0.01 (0.01)	<0.01 (0.01)
American robin *Turdus migratorius*	-0.03 (0.04)	-0.02 (0.02)	-0.01 (0.01)	-0.01 (0.01)
Chestnut-sided warbler *Dendroica pensylvanica*	**-0.10 (0.04)***	**-0.05 (0.02)***	**-0.04 (0.02)***	**-0.03 (0.01)***
Magnolia warbler *Dendroica magnolia*	0.07 (0.04)	0.03 (0.02)	0.01 (0.02)	0.01 (0.01)
Black-throated blue warbler *Dendroica caerulescens*	**0.09 (0.04)***	**0.05 (0.02)***	**0.03 (0.02)***	**0.02 (0.01)***
Black-throated green warbler *Dendroica virens*	**0.15 (0.05)****	**0.09 (0.03)****	**0.06 (0.02)****	**0.05 (0.01)*****
Blackburnian warbler *Dendroica fusca*	0.02 (0.04)	0.01 (0.02)	0.01 (0.02)	0.01 (0.01)
Black and white warbler *Mniotilta varia*	0.06 (0.04)	0.03 (0.02)	0.02 (0.02)	0.02 (0.01)
American redstart *Setophaga ruticilla*	-0.04 (0.04)	-0.03 (0.02)	-0.02 (0.01)	-0.02 (0.01)
Ovenbird *Seiurus aurocapilla*	**0.22 (0.07)****	**0.15 (0.05)****	**0.11 (0.03)*****	**0.09 (0.02)*****

Association between spatial autocorrelation and landscape use

At each spatial scale, we aimed to quantify the relationship between the degree of spatial autocorrelation of each species and its landscape use. We predicted that the species that tend to cluster would be the ones with higher probabilities of occurrence within more forested landscapes. We used two types of analyses: linear regressions and the comparative phylogenetic analysis (Sanford et al. 2002). The latter analysis is performed when comparing closely related species, since they may share traits or adaptations through common ancestry. This situation creates a problem of dependence among species when using traditional correlation or regression analyses (Felseinstein 1985). However, the results were similar independently of the method that was used. We thus report hereafter only the results calculated with the correlations. Since habitat variables were not incorporated into the landscape use analyses, we performed the regressions with the location data from all the sampling stations.

RESULTS

In analyses that ignored spatial components in habitat variables, 85.7% of the species (n = 14) significantly aggregated their territories in at least one spatial scale (Table 2). Only the Black-capped Chickadee (*Poecile atricapillus*) showed negative autocorrelation. Seven species autocorrelated their territories at all spatial scales (Table 2) while the location of five additionnal species was spatially autocorrelated in at least one spatial scale (Table 2).

After controlling for local habitat, nine out of 14 species showed significant spatial autocorrelation in their occurrence data in at least one spatial scale (Table 3). Again, the Black-capped Chickadee was the only species with significant negative autocorrelation. Five species showed significant positive autocorrelation at all spatial scales (Table 3). Furthermore, the occurrence of three species was positively autocorrelated at some spatial scales (Table 3).

Our point count stations were located in landscapes with a range of forest cover at each spatial scale (Fig. 3). Landscapes with less than 50% of forest cover surrounded between 47% and 62% of the point count stations. The Black-throated Green Warbler (*Dendroica virens*), and the Ovenbird (*Seiurus aurocapilla*) were associated significantly to forest cover area at all spatial scales (Table 1). The Yellow-bellied Sapsucker (*Sphyrapicus varius*), the Chestnut-sided Warbler (*Dendroica pensylvanica*), and the Black-throated Blue Warbler (*Dendroica caerulescens*) tended to occur more frequently in forested landscapes. The occurrence of other species were not associated significantly to landscape composition at the spatial scales that were measured.

Table 2. Spatial autocorrelations of species occurrence as indicated by Moran's *I* correlograms. All sampling stations were included in the analyses. Negative Moran's *I* values indicate regular arrays, whereas positive values indicate clusters. Results of test: * p<0.05, ** p<0.01, *** p<0.001.

Species	250 m	350 m	450 m	550 m
Yellow-bellied sapsucker *Sphyrapicus varius*	**0.16 ****	**0.12 ****	**0.07 ****	**0.07 ****
Red-eyed vireo *Vireo olivaceaus*	**0.27 *****	**0.27 *****	**0.17 *****	**0.17 *****
Black-capped chickadee *Poecile atricapillus*	-0.07	**-0.11 ****	-0.03	-0.03
Veery *Catharus fuscescens*	0.10	0.06	**0.06 ***	**0.06 ***
Hermit thrush *Catharus guttatus*	**0.20 *****	**0.20 *****	**0.17 *****	**0.17 *****
American robin *Turdus migratorius*	<0.001	0.02	0.02	0.01
Chestnut-sided warbler *Dendroica pensylvanica*	**0.16 ****	**0.13 *****	0.05	0.05
Magnolia warbler *Dendroica magnolia*	**0.26 *****	**0.23 *****	**0.24 *****	**0.23 *****
Black-throated blue warbler *Dendroica caerulescens*	0.09	**0.09 ***	0.02	0.02
Black-throated green warbler *Dendroica virens*	0.07	0.04	0.04	0.04
Blackburnian warbler *Dendroica fusca*	**0.16 ****	**0.12 ****	**0.10 *****	**0.09 *****
Black and white warbler *Mniotilta varia*	0.09	**0.09 ***	0.05	**0.06 ***
American redstart *Setophaga ruticilla*	**0.18 *****	**0.14 *****	**0.16 *****	**0.16 *****
Ovenbird *Seiurus aurocapilla*	**0.20 *****	**0.16 *****	**0.12 *****	**0.12 *****

Table 3. Spatial autocorrelations of species occurrence as indicated by Moran's *I* correlograms. Only the stations located within the species's appropriate habitat (as calculated with adaptive kernels) were included in the analyses. Negative Moran's *I* values indicate regular arrays, whereas positive values indicate clusters. Results of test: * p<0.05, ** p<0.01, *** p<0.001.

Species	250 m	350 m	450 m	550 m
Yellow-bellied sapsucker *Sphyrapicus varius*	0.14	0.10	0.05	0.05
Red-eyed vireo *Vireo olivaceaus*	**0.22 *****	**0.22 *****	**0.14 *****	**0.14 *****
Black-capped chickadee *Poecile atricapillus*	-0.08	**-0.13 ****	-0.02	-0.03
Veery *Catharus fuscescens*	0.09	0.04	0.05	0.05
Hermit thrush *Catharus guttatus*	**0.21 *****	**0.21 *****	**0.17 *****	**0.17 *****
American robin *Turdus migratorius*	0.02	0.02	0.02	0.02
Chestnut-sided warbler *Dendroica pensylvanica*	**0.16 ****	**0.13 ****	0.05	0.05
Magnolia warbler *Dendroica magnolia*	**0.30 *****	**0.26 *****	**0.24 *****	**0.23 *****
Black-throated blue warbler *Dendroica caerulescens*	0.07	0.07	0.01	0.01
Black-throated green warbler *Dendroica virens*	0.06	0.03	0.04	0.04
Blackburnian warbler *Dendroica fusca*	**0.16 ***	**0.13 ****	**0.10 ****	**0.10 ****
Black and white warbler *Mniotilta varia*	0.08	**0.11 ****	**0.06 ***	**0.07 ***
American redstart *Setophaga ruticilla*	**0.22 *****	**0.17 *****	**0.19 *****	**0.19 *****
Ovenbird *Seiurus aurocapilla*	**0.16 ****	**0.14 *****	**0.12 *****	**0.12 *****

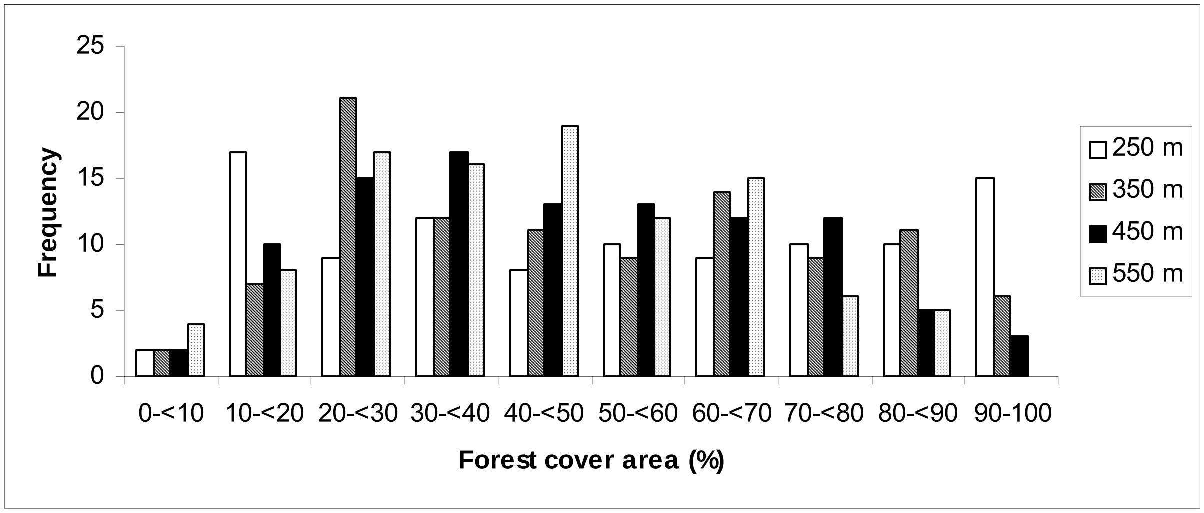

Figure 3. Heterogeneity of landscapes in terms of percentage of forest cover area around 102 point count stations located within 50 km of Québec City (46° 45' N, 71° 20' O), Québec, Canada. Forest cover area is presented for the spatial scales at which the spatial autocorrelation of bird occurrence was measured.

There was no significant relationship between spatial autocorrelation and landscape use at any of the spatial scales that were studied (Fig. 4). We thus measured the power of our analyses for each spatial scale (Table 4). For each spatial scale, we simulated 5000 linear regressions. To calculate the regressions, we used randomly generated data with the same characteristics as our observed data (i.e. parameter estimates and standard errors). The statistical power was low at all spatial scale (5-10%).

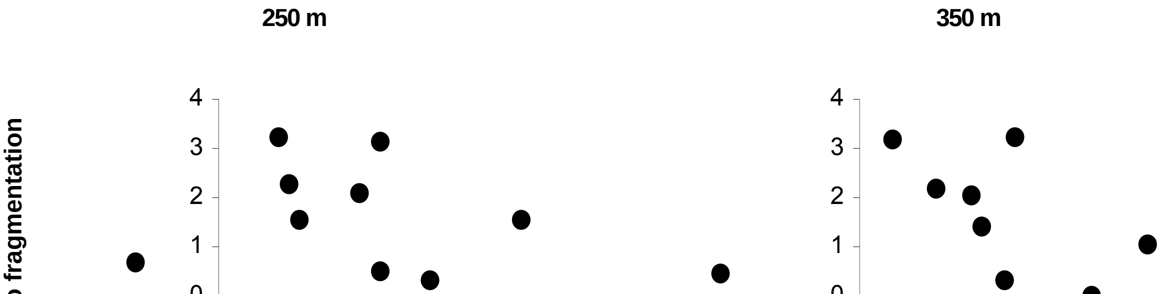

Figure 4. Index of sensitivity to fragmentation (probability of occurrence in relation with forest cover calculated with logistic regressions) and spatial autocorrelation of occurrence (calculated with Moran's *I* coefficient) of 14 forest bird species, within 50 km of Québec City (46° 45' N, 71° 20' O), Québec, Canada. Each dot represents a species.

Table 4. Power of simulated 5000 regressions randomly generated from data with the same characteristics as the observed data (i.e. parameter estimates and standard errors).

Spatial scale	Observed effect size	Power
250 m	-2.5	0.10
350 m	-2.6	0.05
450 m	-4.1	0.10
550 m	-3.7	0.09

DISCUSSION

Our objectives were to document spatial autocorrelation at small spatial scales for the greatest number of forest bird species, and to measure the relationship between spatial autocorrelation and landscape use for these species. Most species considered showed significant spatial autocorrelation on at least one spatial scale. However, the degree of spatial autocorrelation could not be used to predict landscape occupancy patterns.

Of the species studied, more than 71% aggregated their territories. Except for the Black-capped Chickadee (*Poecile atricapillus*), all autocorrelations were positive. In the case of the Black-capped Chickadee, a negative autocorrelation likely indicates territorial spacing at a scale comparable to distance lags used. Indeed, chickadee territory size can reach 5 ha while the territory size of the other species studied is generally ≤ 1 ha (Gauthier and Aubry 1996). Four of the species that we studied showed no spatial autocorrelation: the Veery (*Catharus fuscescens*), the American Robin (*Turdus migratorius*), the Black-throated Blue Warbler (*Dendroica caerulescens*), and the Black-throated Green Warbler (*Dendroica virens*). The American Robin stands out among the species considered because it defends small territories (0.1-0.3 ha; Young 1951; Eiserer 1976). For this species, territories may be aggregated at spatial scales smaller than those that we investigated. The Veery, the Black-throated Blue Warbler, and the Black-throated Green Warbler are generally considered to be strongly associated with local habitat features (Bertin 1977; Paszkowski 1984; Robbins et al. 1989; Holway 1991; Steele 1992; 1993; Robichaud and Villard 1999). Such associations may have driven the occupancy pattern of these species.

Other recent studies (Drolet et al. 1999; Lichstein et al. 2002a; 2002b) have detected spatial autocorrelation in species occurrence and abundance even after controlling for the spatial pattern of habitat variables. For example, Lichstein et al. (2002b) found that the abundance of Black-throated Blue Warbler was significantly autocorrelated at the scale of 500-1000 m. In the same study, the abundance of the Chestnut-sided Warbler was not spatially autocorrelated at small spatial scales, while we found that Chestnut-sided Warbler males aggregated their territories. In another study, Veery's abundance was significantly autocorrelated at small spatial scale (Lichstein 2002a). Furthermore, Drolet et al. (1999) found that Magnolia Warbler's distribution was significantly autocorrelated within 1250 m. Most results from these other studies are similar to what we measured when all stations were included in the analyses. Indeed, 85.7% of the species we studied were spatially autocorrelated. However, when only the stations located within each species' appropriate habitat were included in the analyses, only 71% of the species studied showed spatial autocorrelation. For example, the occurrence of the Yellow-bellied Sapsucker (*Sphyrapicus varius*) was spatially autocorrelated at all spatial scales when all the stations were included in the analyses. But no spatial autocorrelation was found after controlling for the habitat of the Yellow-bellied Sapsucker. This suggests that the Yellow-bellied Sapsucker's distribution reflects local habitat variables. Our results show that this might also be the case for the Veery and the Black-throated Blue Warbler.

Earlier studies have speculated that aggregative behaviour may reflect autocorrelated habitat variables (Brown et al. 1995). We cannot rule out that the spatial aggregations of territories of this study may reflect patterns of autocorrelations in local habitat variables that were not detected by our vegetation surveys. However, we believe that our vegetation surveys accurately portray the habitat of our target species. Indeed, kernel analyses selected stations according to species' preference in habitat. For example, different stations were selected for species associated with edges than for species associated with mature cover. Hence, the observed aggregative pattern may be indicative of a widespread phenomenon in songbird populations.

To our knowledge, our study is the first attempt to link spatial autocorrelation and landscape occupancy patterns. Even though we did not find a significant relationship, our results may be relevant for the management of several species of songbirds in more fragmented landscapes. For example, five of the species considered (the Red-eyed Vireo [*Vireo olivaceus*], the Hermit Thrush [*Catharus guttatus*], the Magnolia Warbler [*Dendroica magnolia*], the American Redstart [*Setophaga ruticilla*], and the Ovenbird [*Seiurus aurocapilla*]) aggregated their territories at all spatial scales. Several studies have found a negative impact of a decrease in forest cover on the distribution or fecundity for most of these species (Villard et al. 1993; Donovan et al. 1995; Robinson et al. 1995; Trzcinski et al. 1999, Bayne and Hobson 2001). This suggests that, in order to aggregate their territories, the species with reduced distribution of fecundity need forest fragments with a minimum radius of 550 m. Furthermore, three other species, the Chestnut-sided Warbler (*Dendroica pensylvanica*), the Blackburnian Warbler (*Dendroica fusca*), and the Black and white Warbler (*Mniotilta varia*) showed territorial clustering for at least one spatial scale. The results of our spatial autocorrelations also suggest management guidelines for these other species that may be of conservation concern. Hence, conservation of large forest patches may be required for the inclusion of territory clusters of most species.

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Chapitre 4

Does the presence of conspecifics influence settlement into territories by ovenbirds?

Bourque, J. et A. Desrochers. **Does the presence of conspecifics influence settlement into territories by ovenbirds?** Sera soumis à *Condor*. Centre de recherche en biologie forestière, Pavillon Abitibi-Price, Université Laval, Québec, Qc, G1K 7P4, Canada. *Ce chapitre est le fruit du travail du candidat. André Desrochers a participé à l'élaboration de l'idée de base de ce chapitre et à la réalisation de certaines analyses statistiques.*

Résumé

La proximité des voisins conspécifiques pourrait donner des avantages aux individus d'espèces territoriales. Cependant, l'influence de la présence des voisins conspécifiques a rarement été mesurée lors des études portant sur la colonisation des territoires. Nous avons testé si les mâles Paruline couronnée (*Seiurus aurocapilla*) s'installeraient préférablement près de conspécifiques. Nous avons manipulé expérimentalement les densités et testé si la colonisation de territoires vacants par les individus sans territoire arrivaient plus fréquemment en présence de voisins conspécifiques. Il n'y avait pas de relation significative entre la probabilité de colonisation par les individus sans territoire et la présence ou le nombre de voisins conspécifiques. Lorsque les voisins conspécifiques étaient absents, les individus sans territoire ont colonisé 33.3% des territoires vacants ($N = 33$). Une proportion similaire de territoires vacants (34.5%, $N = 58$) ont été colonisés lorsque les voisins conspécifiques étaient présents. Nos résultats montrent que le nombre ou la présence de voisins conspécifiques n'influence pas la colonisation de territoires vacants par les mâles sans territoires. Par contre, avant l'acquisition des territoires, le choix d'une région générale de résidence par les individus sans territoire pourrait être facilité par les voisins conspécifiques.

Abstract

The proximity of conspecifics may provide benefits to individuals of non-gregarious species. So far, the effects of conspecific presence have seldom been addressed in studies of songbird territory settlement. We tested whether male ovenbirds (*Seiurus aurocapillus*) would settle preferentially near conspecifics. We used experimental removals to test whether the colonization of territories by floaters was more likely to occur in the presence of conspecific males than in their absence. There was no significant relationship between settlement probability by floaters and presence or number of residual males. When conspecifics were absent, floaters settled 33.3% of vacant territories ($N = 33$). A similar proportion of vacant territories (34.5%, $N = 58$) were settled when conspecifics were present. Our results show that once a male floater has chosen a general area of residency, the number or presence of conspecific neighbours does not affect its settlement of vacant territories. However, before territory acquisition, the choice of a general area of residency by floaters may be facilitated by conspecific neighbours.

INTRODUCTION

Animals, particularly those that are gregarious, often survive and reproduce better in the proximity of conspecifics (Allee 1951; Stephens and Sutherland 1999; Clobert et al. 2001). For example, many studies spanning several taxa have suggested that predators were less successful when attacking large groups (Kenward 1978; Bildstein 1983; Stephens and Sutherland 1999). Additionally, for territorial species living in colonies or groups, defense costs against conspecifics or heterospecifics are lower for central individuals than for individuals located at the edge of the group (Robertson et al. 1979; Gross and MacMillan 1981; Meadows 1995).

Recent studies on non-gregarious species have revealed unexpected benefits of the proximity of conspecifics (Courchamp et al. 1999; Stephens and Sutherland 1999; Stamps 2001). For example, the proximity of conspecific territories can facilitate the assessment of habitat suitability from information obtained by the neighbours' reproductive activity (Desrochers and Magrath 1993; Doligez et al. 2002) or population density (Doligez et al. 2004). Several authors hypothesized that such "public information" and other benefits from nearby conspecifics will promote settlement in clusters in territorial birds (e.g., Doligez et al. 1999; Greene and Stamps 2001; Wagner and Danchin 2003). If benefits from the presence of conspecifics outweigh costs such as competition (e.g., Morris 2003) and cuckoldry (Møller and Birkhead 1993; Petrie and Kempenaers 1998), then the presence of conspecifics should facilitate settlement by birds in search of a territory. The conspecific attraction hypothesis has rarely been tested experimentally with "non-colonial" songbirds, using playback experiments (Alatalo et al. 1982; Muller et al. 1997; Ward and Schlossberg 2004) or direct measures of annual immigration/emigration (Doligez et al. 2004).

Ovenbirds (*Seiurus aurocapillus*) are territorial, socially monogamous neotropical migrants that tend to breed in large forest patches (Van Horn and Donovan 1994; Ortega and

Capen 1999; Porneluzi and Faaborg 1999; Bayne and Hobson 2002). Several lines of evidence suggest the potential importance of conspecifics for territory establishment in the ovenbird. In Chapter 3, the occurrence of territorial ovenbird males was spatially autocorrelated at several spatial scales (tested up to, but not above 550 m), even after accounting for variation in vegetation structure and composition. This suggests that ovenbirds do not settle at random. Furthermore, the association of ovenbirds to forest patches usually much larger than their territory (Van Horn and Donovan 1994; Ortega and Capen 1999; Porneluzi and Faaborg 1999; Bayne and Hobson 2002) could result from the need to aggregate (Lichstein et al. 2002).

Here, we address the role of conspecifics during territory settlement in the ovenbird. We tested experimentally whether settlement into new territories is facilitated by the presence of conspecific males in the same forest patch. In many bird species, some inexperienced individuals are prevented from establishing a territory by competitive, territorial males (Smith 1978, Wittenberger 1981, Arcese 1987). Such ‘floaters’ (Knapton and Krebs 1974) are thus excluded from breeding unless a territory becomes available. Studies on floater behavior suggest that floaters range over large areas and that they are at the bottom of dominance hierarchies (Smith 1984). We tested whether the presence of conspecific males influence the probability of settlement by floaters into territories made vacant by experimental removals in the breeding season (hereafter ‘vacant territories’).

METHODS

The study area was located in an agricultural landscape within 50 km of Québec City (46° 45’ N, 71° 20’ O), Québec, Canada. Remaining forest patches within the study area were sharply delimited by either agricultural fields or roads. Forests consisted of mixed-tolerant hardwood dominated by deciduous species such as red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), and sugar maple (*A. saccharum*). Coniferous species included balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*). We selected 63 forest patches each covering 2-10 ha and located in mature (>60 years) maple stands (Fig. 1). These patches were all settled by at least one ovenbird. Our study area corresponded to "shredded" forests (Forman and Godron 1986) and most patches were not isolated but rather were connected at some extent to larger forest stands. Hence, patch size and isolation were not included in the analyses (see below).

We were mostly interested in the influence of two explanatory variables on floater settlement: the occurrence (presence/absence) of conspecifics, and the number of conspecifics. However, variables other than conspecific presence or density may drive settlement decisions in ovenbird males. For instance, because conspecifics are competitors, the presence of conspecifics in a patch could

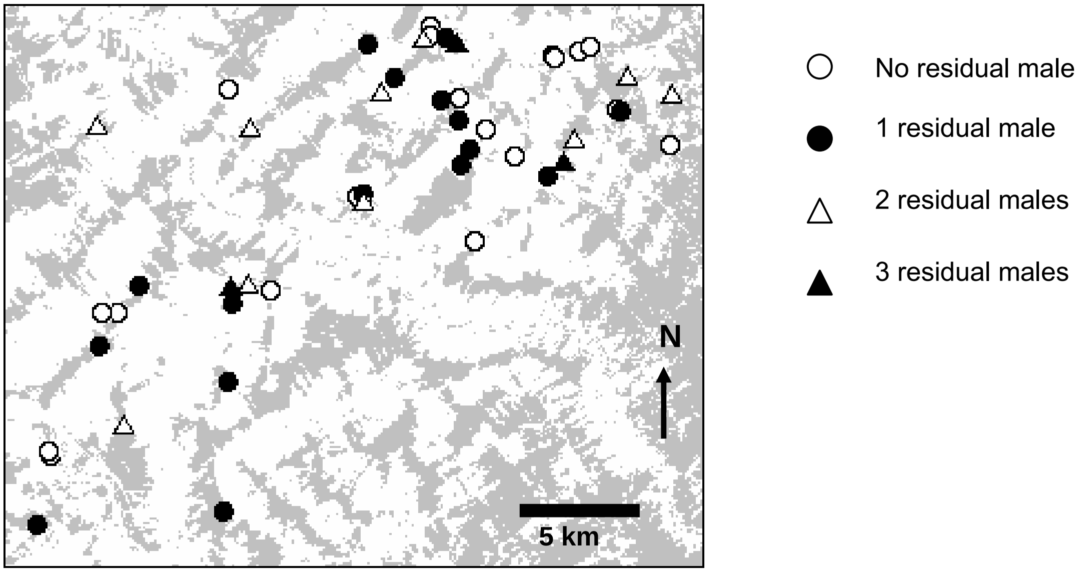

Figure 1: Layout of 63 experimental removal sites over a classified satellite image. Sites are located within 50 km of Québec City (46° 45’ N, 71° 20’ O), Québec, Canada. Mature forest

is represented by the grey areas while the white areas represent all other types of habitat (agricultural fields, roads, human settlements, bodies of water).

discourage floaters to settle in that patch. Furthermore, an increase in forest cover at the landscape scale has been shown to be associated with ovenbird presence (Porneluzi et al. 1993; Wenny et al. 1993; Ortega and Capen 1999; Porneluzi and Faaborg 1999; Bayne 2000). Also, the settlement of migrant species is likely influenced by the occurrence of resident species ("heterospecific attraction hypothesis"; Mönkkönen et al. 1990; 1996; 1997; Timonen et al. 1994; Forsman et al. 1998). Finally, males are likely to be more choosy in their settlement tactics early on in the breeding season, when they are at a relatively low risk of not getting territory at all for that breeding season. Therefore, variables addressing these points were included in our analyses (see below).

The experimental removals were conducted between 25 May and 30 June of 2000 – 2002. We conducted the removals as soon as the number of settled ovenbird males (i.e. that actively defended their territory) levelled off. This helped to ensure that vacant territories would be settled by floaters and not by late-arriving individuals. We are aware that 30 June seems late to measure territorial replacement, but floaters were willing to settle into new territories throughout the duration of the experiment (see Results section). Before the start of this study, we had no information on the spatial scale at which ovenbirds may cluster. Ovenbird territories generally cover < 2 ha (Van Horn and Donovan 1994). Therefore, we arbitrarily delimited a 100-m radius circle within each forest patch. We considered the area demarcated by each of these circles as a ‘neighbourhood’ (*sensu* Stamps 2001). We assumed that individuals in these neighbourhoods would interact with each other on a regular basis. Within each neighbourhood, we removed one to four males (Table 1). Males that were not removed are hereafter designated as residual males. Treatments (with or without residual males) were allocated randomly among neighbourhoods. Captured ovenbird males were individually marked and immediately relocated 25 km from their breeding territory. Immediately before and after the manipulations, mapping of the neighbourhood allowed us to determine the number of conspecific males present.

Table 1: Replacement of territories made vacant after the experimental removals of territorial ovenbirds (*Seiurus aurocapillus*) in an agricultural landscape within 50 km of Québec City (46° 45' N, 71° 20' O), Québec, Canada. Numerators = number of replacement males, denominators = pooled numbers of removed males.

	Residual males				
Vacant territories	0	1	2	3	Total (%)
1	6/20	6/13	2/8	1/1	35.7%
2	2/10	5/10	2/8	0/2	30.0%
3	3/3	1/6	1/3	0/3	33.3%
4		2/4			50.0%
Total	33.3%	42.4%	26.3%	16.7%	34.1%

Each neighbourhood was revisited on the first and second day after the removal. We focused on short-term floater settlement in order to visit as many forest patches as logistically possible during the course of the study. Furthermore, in a concurrent study (Desrochers et al., unpublished data), we measured the return rate of all relocated males and noted that 21% of individuals returned to their territories within 5 days of their capture. But no relocated males reclaimed their territories during the first two days after the manipulations. Each revisit lasted at least an hour. On each revisit, we mapped all singing males in the neighbourhood and played a recording of ovenbird territorial songs for 5 min to encourage settlers to reveal themselves (Marion et al. 1981). Each male detected in the neighbourhood were carefully checked for leg bands during the revisits. This helped ensure that the relocated males had not returned. During each revisit, we also recorded the occurrence of resident species [i.e. black-capped chickadee (*Poecile atricapillus*), white-breasted nuthatch (*Sitta carolinensis*), and red-breasted nuthatch (*Sitta canadensis*)].

The Canadian Wildlife Service obtained LANDSAT-TM satellite images of the entire study area in 1993-1994 and classified these images into forest and non-forest habitats (Bélanger and Grenier 1998). We imported the satellite images into a Geographic Information System (ESRI, 1996). We assumed that the configuration of the study area did not change between 1993-1994 and 2000-2002 based on observations in the field. Total forest cover area was calculated in 500-m radius circles centered on each neighbourhood (Rempel 2000). Ovenbird males generally defend territories < 2 ha (Van Horn and Donovan 1994). Thus, we assumed that 500-m radius circles would include landscape characteristics relevant to the perceptual range of breeding male ovenbirds.

We used logistic regressions (SAS Institute Inc. 1999) to model the relationship between the proportion of new settlers within each neighbourhood and explanatory variables (Table 2). We considered neighbourhoods, not individual birds, as the experimental units. Two separate logistic regressions measured the influence of the occurrence (presence/absence) of residual males in the neighbourhoods and of the number of residual males in the neighbourhoods, respectively. Other explanatory variables were included in both logistic regressions. These other variables were: the number of territorial males before removals in the neighbourhoods (hereafter initial density), Julian date, occurrence of resident species, quantity of forest within a 500-m radius of the neighbourhoods, and year (2000, 2001, or 2002). Before conducting our analyses, we noticed a possible interaction between year and the presence of residual males (Fig. 2). Hence, this interaction was also included as an explanatory variable in the first logistic regression.

RESULTS

We captured and relocated 91 males in 63 neighbourhoods. Among these neighbourhoods, 41.3% did not contain any residual males after the manipulations, 33.3% contained one residual male, 20.6% contained two residual males, and 4.8% had three residual males (Fig. 1). In 5 of the revisits, an unbanded individual was present in a vacated territory but the number of territorial males in the neighbourhood remained unchanged. Thus, we assumed that a settled neighbour had annexed the vacant territory to its own territory. These cases were not considered to be new settlements.

There was no significant relationship between settlement probability by floaters and presence of residual males (Table 2). When conspecifics were absent, floaters settled 33.3% of vacant territories. When conspecifics were present, results were very similar, with 34.5% of vacant territories settled. The number of residual males also did not influence settlement probability (Table 2). In both regressions, initial density of conspecifics did not affect significantly the probability of settlement of floaters (Table 2). Julian date, occurrence of resident species, forest cover, year, and the interaction between year and presence of residual males were all non-significant (Table 2).

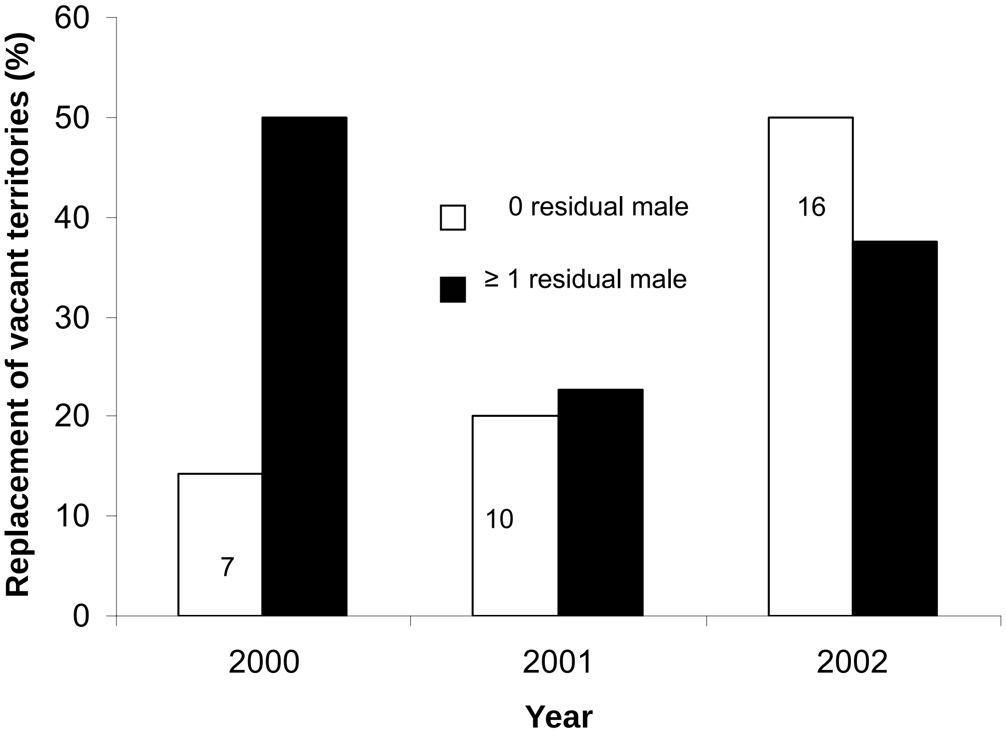

Figure 2: Percent replacement of territories made vacant after the experimental removals of territorial ovenbird (*Seiurus aurocapillus*) males. The removals were performed in an agricultural landscape within 50 km of Québec City (46° 45’ N, 71° 20’ O), Québec, Canada. Number of vacant territories is indicated above bars.

Table 2. Variables explaining the probability of settlement by floaters into territories made vacant by experimental removals of breeding ovenbird (*Seiurus aurocapillus*) males. Removals were performed in an agricultural landscape within 50 km of Québec City (46° 45’ N, 71° 20’ O), Québec, Canada.

Variables	df	X^2	P
First model			
Occurrence of residual males [1]	1	0.49	0.49
Initial density [2]	1	0.48	0.49
Julian date	1	0.26	0.61
Occurrence of resident species [3]	1	2.06	0.15
Forest cover [4]	1	1.83	0.18
Year	2	2.33	0.31
Year x occurrence of residual males	2	1.84	0.40
Second model			
Number of residual males	1	0.01	0.93
Initial density	1	0.11	0.74
Julian date	1	0.25	0.62
Occurrence of resident species	1	1.99	0.16
Forest cover	1	2.77	0.10
Year	2	2.19	0.33

[1] Males that were not removed

[2] Number of territorial males before removals

[3] Black-capped chickadee (*Poecile atricapillus*), white-breasted nuthatch (*Sitta carolinensis*), and red-breasted nuthatch (*Sitta canadensis*)

[4] Forest cover area (in ha) calculated in 500-m radius circles

DISCUSSION

We tested whether the probability of replacement of vacant territories would be greater with the occurrence of conspecific neighbours than without. There was no significant effect of the occurrence or number of conspecific neighbours within 100 m on the probability of replacement by floaters, despite considerable sampling effort. We consider that statistical power was not a cause for concern because the observed frequencies of settlements of removal and control plots were almost identical and sample sizes were reasonably high. Even though the occurrence of conspecifics did not affect the probability of replacement of vacant territories, the effect size we observed could be used in future comparisons among similar studies. This would likely help the understanding of interspecific variation in how social neighbourhoods influence territorial behaviour and settlement decisions. Furthermore, the fact that ovenbird floaters replaced vacant territories rapidly suggests that they might use conspecifics to choose larger tracts of habitat and not specific vacancies.

Our results contrast with those obtained in previous work on non colonial species (Alatalo et al. 1982; Muller et al. 1997; Doligez et al. 2004; Ward and Schlossberg 2004). These studies concluded that occurrence or density of conspecifics may be a useful cue of habitat suitability for both adults and yearlings. These differences may stem from methodology: most of these studies used either playbacks to attract floaters or measured settlement rate in nest boxes while we conducted experimental removals. Although adult birds have been shown to use conspecific presence or density in their settlement decisions (Doligez et al. 2004), conspecifics may be an especially important cue of habitat suitability for yearling birds. Indeed, yearlings may face time constraints that would limit severely the scope and duration of their prospecting behaviour. Thus, settlement decisions of yearlings is likely based primarily on conspecific density. On the other hand, older adults may have better access to other cues of patch suitability such as conspecific breeding success in previous years (Doligez et al. 2004). Settlement decisions may therefore be based on different criteria for yearlings and older adults in the ovenbird. We do not have reliable data on the age of replacement birds, but it is possible that they included a significant proportion of non-juveniles. Such a situation could explain the observed lack of relationship between conspecific density and floater settlement.

The only other removal experiment performed on the ovenbird suggests that floaters are more prevalent in habitats with high conspecific density (Bayne and Hobson 2001). In that study, the age of replacement birds was not assessed. Furthermore, the number of residual males was confounded with the amount of surrounding forest. In their contiguous forest sites, vacant territories all had at least one residual conspecific neighbour, whereas in their agricultural landscape sites the majority of vacant territories did not have a conspecific neighbour. Differences in initial density amongst the sites also could have explained the resulting replacement probability by floaters observed by Bayne and Hobson (2001).

Settlement decisions are likely complex and probably involve the integration of multiple cues. For example, when settling into higher density areas, individuals may face several potential costs, including intraspecific competition (Rosenzweig 1985; 1991; Sutherland and Parker 1992; Halama and Dueser 1994; Ovadia and Abramski 1995; Morris 1996; 2003; Sutherland 1996; but see Holmes et al. 1996; Petit and Petit 1996) and an increase in cuckoldry risk (Møller and Birkhead 1993; Petrie and Kempenaers 1998; but see Westneat and Sherman 1997; Thusius et al. 2001). Thus, there might be a tradeoff between settling into higher density areas, even if density serves as an indicator of habitat suitability, and increased costs. However, we interpret two of our results as pointing against that explanation. First, floaters were willing to settle territories late in the breeding season. This may indicate that the risk of zero reproduction is greater than the potential increase of costs. Second, the initial density of conspecifics did not influence the settlement probability of floaters. If high density populations present increased risks of intraspecific competition or cuckoldry for settling individuals, one might expect floaters to be less prevalent within these populations before the experimental manipulations. Another point to consider is that although males may face an increased risk of cuckoldry in high density populations, opportunities for extra-pair mating also increase (Gibbs et al. 1990; Wagner 1993). In fact, Norris and Stutchbury (2001) suggested that territorial establishment likely depends on the availability of extra-pair partners for the hooded warbler (*Wilsonia citrina*), a territorial and socially monogamous passerine.

A possible limitation of this study is that the range of residual male number was too restricted (0 - 3 residual males within 100 m) to detect a significant difference. It could also be argued that for some reason, the study area was saturated with ovenbird floaters. Such a situation could have hidden any pattern associated with conspecific presence. Saturation seems unlikely since floaters settled only 34.1% of the territories that were made available to them. This probably does not result from the monopolization of certain areas by "despotic" floaters since we recorded numerous instances in which adjacent vacant territories were settled by different floaters. The same observation was recorded in another removal experiment with ovenbird males (Bayne and Hobson 2001). Indeed, Bayne and Hobson (2001) found that floaters settled 50% of the territories made available to them.

CONCLUSION

Our results show that once an ovenbird male floater has chosen a general area of residency, the number or presence of conspecific neighbours at close range does not affect its settlement of vacant territories. These results may depend on the spatial scale at which a neighbourhood is defined. Alternatively, if floaters in our study area consisted mostly of older males, settlement decisions may have been based on cues other than conspecific presence or density. Indeed, conspecific territory holders may reflect habitat suitability mostly for first-time breeders (Doligez et al. 2004; Kiester and Slatkin 1973; Stamps 1987; 1988; 1994; Smith and Peacock 1990; Ray et al. 1991; Reed and Dobson 1993). Future experimental studies should thus try to ascertain (1) whether the presence or number of conspecifics might be associated with the choice of a general area of residency by floaters, and (2) the relative roles of conspecific presence, density and breeding success in settlement decisions of yearlings and older breeders.

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Chapitre 5

Male population density and settlement decisions of female ovenbirds

Bourque, J. et A. Desrochers. **Male population density and settlement decisions of female ovenbirds.** Sera soumis à *Canadian Journal of Zoology*. Centre de recherche en biologie forestière, Pavillon Abitibi-Price, Université Laval, Québec, Qc, G1K 7P4, Canada. *Ce chapitre est le fruit du travail du candidat. André Desrochers a participé à la réalisation de certaines analyses statistiques.*

Résumé

Le succès d’appariement de la Paruline couronnée (*Seiurus aurocapilla*) est généralement associé aux caractéristiques de l’habitat à l’échelle locale et à l’échelle du paysage. Par contre, la densité des mâles conspécifiques pourrait également influencer la colonisation des femelles et confondre les résultats ci-dessus. Malgré cela, la densité des mâles conspécifiques a rarement été incorporée dans les études portant sur le succès d’appariement des passereaux forestiers. Nous avons testé si les femelles Paruline couronnée préféraient s’installer dans les sites avec de fortes densités de mâles conspécifiques. Nous avons utilisé les données de 10 études publiées pour mesurer la relation entre le succès d’appariement et la densité de mâles conspécifiques en tenant compte de la quantité de couvert forestier autour des sites d’étude. La proportion de mâles appariés augmentait avec la densité des mâles conspécifiques, même après avoir tenu compte du couvert forestier. Les populations avec des densités élevées semblent donc attirer les femelles Paruline couronnée. Ceci suggère que les femelles choisissent leur territoire de reproduction au moins en partie en fonction de la densité des mâles conspécifiques.

Abstract

Ovenbird (*Seiurus aurocapilla*) pairing success is associated with habitat characteristics at landscape and local scales. But male conspecific density may also influence female settlement decisions and confound the above results. However, male population density is seldom incorporated in models investigating pairing success of forest songbirds. Here, we tested whether female Ovenbirds would settle preferentially in the presence of high population density of conspecific males. We used published data from 10 studies to measure the relationship between pairing success and conspecific male density while accounting for forest cover area around the study sites. The proportion of paired Ovenbird males increased with conspecific density after accounting for forest cover. Thus, high-density populations seem attractive to Ovenbird females, suggesting that the female choice of breeding habitat is likely driven at least in part by male population density.

INTRODUCTION

Forest fragmentation generally results in a change in the configuration of residual forest patches combined with habitat loss (Koford et al. 1994). There is both direct (Robinson et al. 1995; Zanette and Jenkins 2000) and indirect (Rich et al. 1994; Walters et al. 1999) evidence that forest fragmentation is associated with a decrease in the breeding success of songbirds occurring in forest remnants (but see Friesen et al. 1999). This, in turn, may affect negatively population densities (Porneluzi and Faaborg 1999; Stephens et al. 2003) unless surplus individuals from nearby productive areas immigrate into fragmented forests (Pulliam 1988; Pulliam and Danielson 1991; Donovan and Lamberson 2001).

In the context of forest fragmentation, the key mechanisms behind breeding success need to be understood if remedial steps are to be successful. For example, if the pairing success of forest-dwelling songbirds is lower in isolated woodlots (reviewed in Bélisle et al. 2001), increasing connectedness between fragments may improve demographic responses. On the other hand, lower fitness in fragmented landscapes may stem from a lack of suitable habitat (Rodewald and Yahner 2000). If this is the case, managers would need to conserve remaining patches of suitable habitat while creating larger areas of preferred habitat.

Breeding success includes several components such as pairing success, fecundity, and survival of offspring. Of these components, pairing success occupies a unique position since a low pairing success suggests that males and females have limited access to habitat patches, or respond to different stimuli when selecting their breeding territories (assuming no female-biased mortality in fragmented landscapes). In the latter case, one hypothesis suggests that females, but not males, recognize that forest fragments contain lower-quality habitat than contiguous forests (Probst and Hayes 1987; Villard et al. 1993; Van Horn et al. 1995; Burke and Nol 1998). Or, females may prefer aggregated males and avoid solitarily males (the hidden-lek hypothesis; Wagner 1997; Smith and Peacock 1990). Areas too small or fragmented to accommodate several territories may thus be bypassed by females.

In studies pertaining to the effects of forest fragmentation on pairing success of songbirds, one of the most studied species is the Ovenbird. Pairing success of Ovenbird males is lower in fragmented forests relative to contiguous ones (Porneluzi and Faaborg 1999; Burke and Nol 2000; Lee et al. 2002). Paired Ovenbirds are also more prevalent in large forest patches versus small ones (Villard et al. 1993; Van Horn et al. 1995; Lee et al. 2002). Most studies on Ovenbird pairing success have focused on the relationship between pairing success and habitat characteristics (Van Horn et al. 1995; Burke and Nol 1998; Lee et al. 2002). However, in Chapter 3, we found that Ovenbird males do not settle their territories at random but rather tend to cluster their territories at small spatial scales (< 550 m), even after accounting for habitat. This suggests that pairing success may rest on hitherto unadressed behavioural processes (Lima and Zollner 1996) such as female preference for aggregated males (Wagner 1997).

Here, we address the role of male population density during territory settlement from the perspective of females in the Ovenbird. We used published data to measure the relationship between pairing success and conspecific male density, while accounting for forest area. A positive relationship between pairing success and density would indicate that females are attracted to areas with high male density, resulting in relatively high pairing success in those areas.

METHODS

To be included in our review, a study needed to have measured both Ovenbird pairing success and population density. We selected studies that quantified density with either spotmapping or total mapping (Bibby et al. 1992). Ten Ovenbird studies satisfied our criteria and were included in our review (Table 1). In the papers we reviewed, most of the study sites were grouped into categories, which made it difficult to compare the data across studies. We thus contacted the researchers (Table 1) and, for each individual site within each study, asked the researchers to provide the following information: proportion of paired males, density (males / 10 ha of habitat), and year. In these studies, study sites were generally assigned to a landscape type (either fragmented or contiguous forests). We kept these classifications but also asked the researchers to provide a more quantitative assessment of forest cover area around their study sites, if such information was available. Hence, we asked researchers to classify each of their study plot according to the surrounding forest cover within 1 km. We provided the researchers with three categories of forest cover: low (0-33%), moderate (34-66%), or high (67-100%). The number of sites for each study varied between 3 and 16 (mean = 8.2) for a total sample size of 81 study sites, with some sites having data from multiple years. Of these, 64 sites could be classified according to the amount of surrounding forest cover.

Table 1. Estimates of Ovenbird density (males / 10 ha) and pairing success in contiguous and fragmented forests in published studies. Pairing success consists in the proportion of paired males within each landscape type.

Density in contiguous forest	Density in fragmented forest	% paired in contiguous forest	% paired in fragmented forest	State/province	Reference
7.7	1.9	84.9	53.6	New Jersey	Wander 1985
6.9	3.0	66.8	50.0	Pennsylvania	Porneluzi et al. 1993
1.4	0.8	55.0	15.4	Missouri	Van Horn et al. 1995
2.3	2.2	81.4	56.5	New Brunswick	Sabine et al. 1996
9.3	-	85.0	-	Vermont	Ortega and Capen 1999
2.2	1.6	67.0	66.0	Missouri	Porneluzi and Faaborg 1999
4.8	-	78.1	-	Pennsylvania	Rodewald and Yahner 2000
9.4	4.8	92.0	76.2	Saskatchewan	Bayne and Hobson 2001
4.7	5.0	76.6	71.1	New Brunswick	Bourque and Villard 2001
4.3	-	89.3	-	Massachusetts	King and DeGraaf 2002

Since some sites were surveyed during several years, we analysed the data with a repeated-measures design fitted using the GENMOD procedure of SAS 8.01 (SAS Institute Inc. 1993). Instead of using a variable that contains the response value for each observation, we specified the response variable as the ratio of two variables: the number of mated males and the total number of males (the events/trials form; Stokes et al. 1995). Density and landscape type were the explanatory variables. Another logistic regression was performed with the variable landscape type replaced by the amount of forest cover surrounding each site (as classified by the researchers).

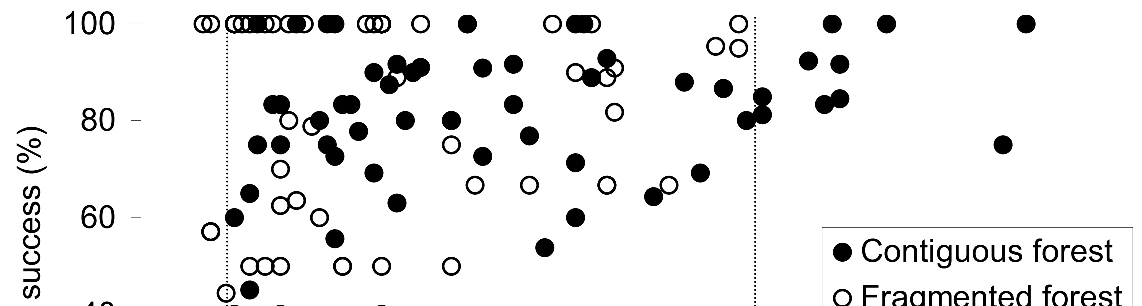

Figure 1. Data from published studies showing that Ovenbird pairing success increases with male density in contiguous and fragmented forests. Each point represents a study site during a single year. Statistical analyses were performed on (1) all the data points, and (2) the data included in the interval delimited by the vertical lines.

We noticed that the distribution of male density might be confounded with the category of landscape type. The highest densities (13.6 percentile) were found exclusively in contiguous forests, whereas the lowest densities (11.1 percentile) were present only in fragmented forests (Fig. 1). We believe there may be two reasons for this observation. First, researchers may unconsciously be unwilling to study low-density populations in contiguous landscapes (even though they may exist) in order to maximize their sampling size. Second, in fragmented landscapes, forest patches may be too small to accommodate high-density populations. Based on this observation, we performed all the analyses a second time but excluded the data points outside the range of male population densities that occurred in both contiguous and fragmented forests. Before this exclusion, density ranged from 0.3 to 11.4 males / 10 ha. After the data were excluded, density ranged from 1.2 to 7.7 males / 10 ha.

RESULTS

We first present the results when all study sites were included. Pairing success increased with density ($X^2_1 = 12.47$, $P = 0.0004$) but not with landscape type ($X^2_1 = 2.28$, $P = 0.13$). In the model with the amount of forest cover around the study sites, the proportion of paired males increased with density ($X^2_1 = 8.01$, $P = 0.005$). Males in sites surrounded by moderate amounts of forest cover did not attract more females compared to sites with low amounts of forest cover ($X^2_1 = 2.54$, $P = 0.11$). However, pairing success increased in sites with high amounts of forest cover compared to sites with low forest cover ($X^2_1 = 4.26$, $P = 0.04$).

When the analyses were confined to data points inside the range of male population densities that occurred in both contiguous and fragmented forests, pairing success still increased with conspecific male density ($X^2_1 = 6.57$, $P = 0.01$) but not with landscape type ($X^2_1 = 0.81$, $P = 0.48$). In the model with the amount of forest cover as explanatory variables, the proportion of paired males increased again with density ($X^2_1 = 5.13$, $P = 0.02$) but was not higher in sites with moderate and high amount of forest cover compared to sites with low forest cover (moderate forest cover: $X^2_1 = 2.26$, $P = 0.13$; high forest cover: $X^2_1 = 2.46$, $P = 0.12$).

DISCUSSION

We hypothesized that areas with high male population density would increase the females' settlement rate, leading to the prediction that pairing success increases with male density. Our results supported this prediction. Typically, differences in Ovenbird pairing success among landscapes have been attributed only to the extent of forest fragmentation

(Porneluzi and Faaborg 1999; Burke and Nol 2000; Bayne and Hobson 2001; Bourque and Villard 2001). However, we have shown that the female choice of breeding habitat may also be driven by male population density, irrespective of landscape type. Forest fragmentation may act only indirectly by precluding the clumping of territorial males, thus lowering male population density and, in turn, pairing success.

The apparent female preference for high-density “neighbourhoods” (sensu Stamps 2001) may have been produced in several ways. First, female choice of a mate may occur through the active selection of male characteristics, for example age or size (Villard et al. 1993). The highest quality male in a given area pairs with only one female in a socially monogamous mating system (Westneat et al. 1990). But other females can solicit extrapair copulations provided they have easy access to that favored male. Hence, females may prefer to pair with males that display near the top male (Wagner 1997). Such a situation could lead to the clustering of territorial males in response to female preference for being near the most favored male. Alternatively, females may prefer to appraise males in groups, and thus bypass males that display solitarily (Bradbury 1981). But the isolation of small forest patches by forest fragmentation may preclude the clumping of males, thus rendering these males unattractive to females.

Villard et al. (1993) found in their literature review that pairing success was higher in extensive forests compared to fragmented forests. Since then, most studies that have measured Ovenbird pairing success have also found lower pairing success in fragmented landscapes than in contiguous forests. The results from these studies contrast somehow with ours. We did find that high forest cover influenced positively pairing success, but only when extremes in population density were included in the analyses. We offer several possible explanations for these results. First, in their literature review, Villard et al. (1993) compared the means of pairing success between extensive and fragmented forests. As such, each study had the same weight in their analysis, independently of the number of sites. A study with a disproportionately high number of sites may thus have driven the relationship they found. Second, researchers may unconsciously study extremes in population density in their study area such that the highest densities (whose populations tend to have the highest pairing success) always occur in landscapes with high forest cover. But we have shown that high-density populations (even those in fragmented landscapes) can show high pairing success, while low-density populations (even those in contiguous forests) tend to show low pairing success (Fig. 1).

Our results are not mutually exclusive with ressources-based predictions of distribution patterns. Settlement decisions probably involve the integration of multiple cues of habitat suitability. For Ovenbird males, occupancy patterns have been repeatedly associated with an increase in forest cover at the landscape scale (Porneluzi et al. 1993; Wenny et al. 1993; Ortega and Capen 1999; Porneluzi and Faaborg 1999) and with habitat characteristics at the local scale (Van Horn and Donovan 1994; Burke and Nol 1998). Hence, males may select their territories on the basis of ressources availability while females likely also select where to breed in function of male density. Thus, the decrease in the occurrence of Ovenbird females documented in fragmented forests may result from female selection of conspecific neighbourhoods as a proximate factor. Forest fragmentation may indirectly result in low pairing success simply by lowering territorial aggregation. This, in turn, would decrease male population density which would influence negatively pairing success. In order to increase pairing success in the Ovenbird, our results thus suggest that large forest patches need to be conserved in fragmented forests. Furthermore, females of other species that tend to avoid fragmented forests may also use the presence and density of males in their settlement decisions (e.g. Ward and Schlossberg 2004). Henceforth, studies should incorporate the density of conspecifics in models predicting the effects of forest fragmentation on pairing success of forest songbirds.

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Conclusion générale

Plusieurs espèces de passereaux forestiers connaissent une réduction de leur abondance dans les petits fragments de forêt comparativement aux parcelles de grande superficie (Robbins 1979; Ambuel et Temple 1983; Blake et Karr 1987; van Dorp et Opdam 1987; Blake 1991). Au cours des dernières décennies, de nombreuses études ont tenté de déterminer les causes d'une telle sensibilité à la superficie et à la structure des forêts (Temple et Cary 1988; Andrén 1992; Askins 1995; Robinson et al. 1995; Donovan et al. 1997; Burke et Nol 1998; Roberts et Norment 1999; Zanette et al. 2000). De plus, plusieurs chercheurs préconisent le développement d'outils pour prédire la sensibilité des espèces et pour identifier les espèces à risque (Lima et Zollner 1996; Walters 1998; Desrochers 2003). Ces outils pourraient être basés sur les différences entre les espèces par rapport à leur sensibilité (e.g. Hannon et Schmiegelow 2002; Henle et al. 2004). La présente thèse représente une des premières tentatives de comparaison des causes potentielles de la sensibilité à la structure des forêts entre les espèces de passereaux forestiers à partir de données comportementales.

Théoriquement, le manque de connectivité entre les parcelles de forêt isolées pourrait diminuer la probabilité d'occurrence d'espèces forestières dans les paysages fragmentés (Taylor et al. 1993 ; Fahrig et Merriam 1994). Les chercheurs qui préconisent une meilleure connectivité entre les fragments forestiers sous-entendent que les mouvements des individus sont contraints par les milieux ouverts. Si c'est le cas, la capacité de certaines espèces à explorer et à coloniser les parcelles de forêts isolées pourrait diminuer en milieu fragmenté. Les espèces les plus contraintes dans leurs mouvements devraient donc être moins présentes dans les forêts fragmentées. Cette thèse constitue une des premières tentatives de mesurer quantitativement les capacités de déplacement des migrateurs Néotropicaux. Au premier chapitre, j'ai montré que, sur les dix espèces de passereaux forestiers étudiées, huit avaient moins tendance à traverser les milieux ouverts que les milieux forestiers. Par contre, cette tendance n'était significative que chez deux espèces, soit le Viréo aux yeux rouges (*Vireo olivaceus*) et la Paruline à tête cendrée (*Dendroica magnolia*). D'autre part, la réticence à traverser les milieux ouverts ne permettait pas de prédire la sensibilité à la structure des forêts. Cette absence de corrélation entre la réticence à traverser les milieux ouverts et la sensibilité à la structure des forêts corrobore les résultats de Hannon et Schmiegelow (2002). Dans cette étude, l'abondance des espèces dans des fragments isolés par la foresterie ne pouvait pas être prédite par la propension de ces espèces à traverser les milieux ouverts.

Pour mesurer la capacité des individus à se mouvoir, j'ai utilisé au premier chapitre des enregistrements de cris de houspillage de Mésange à tête noire (*Poecile atricapillus*). Plusieurs espèces de passereaux forestiers sont attirés par le houspillage des Mésange à tête noire (Hurd 1996; Gunn et al. 2000; Turcotte et Desrochers 2002). Ceci permet d'orienter et de contrôler les mouvements des individus sur de courtes distances. Par contre, les cris de houspillage représentent potentiellement une situation risquée pour les oiseaux puisque le houspillage est généralement associé à la présence d'un prédateur. L'utilisation d'enregistrements de cris de houspillage pourrait entraîner un biais si les oiseaux répondent différemment au houspillage en milieu ouvert qu'en forêt continue. Dans le deuxième chapitre, j'ai contredit cette hypothèse en déterminant que la perception du risque associée au houspillage chez le Viréo aux yeux rouges et chez la Mésange à tête noire ne différait pas entre les milieux ouverts et la forêt continue.

La mobilité des passereaux forestiers n'est pas le seul facteur potentiel de sensibilité à la structure des forêts. Les espèces qui ont tendance à regrouper leurs territoires pourraient éviter de coloniser les petites parcelles de forêt (Smith et Peacock 1990; Wagner et Danchin

2003). Ce phénomène a souvent été soupçonné d'exister (Lischtein et al. 2002a), mais son ampleur n'avait jamais été quantifiée avant cette thèse. En effet, en mesurant le degré d'agrégation des territoires chez les passereaux forestiers, j'ai montré dans le troisième chapitre que 85,7% (n = 14) des espèces étudiées avaient tendance à regrouper leurs territoires. Chez trois espèces, soit le Pic maculé (*Sphyrapicus varius*), la Grive fauve (*Catharus fuscescens*) et la Paruline bleue (*Dendroica caerulescens*), le regroupement des territoires semblait suivre la répartition spatiale 'contagieuse' de la végétation locale. Par contre, les autres espèces qui regroupaient significativement leurs territoires le faisaient indépendamment de la répartition spatiale des ressources végétales. Mes résultats sont semblables à ceux d'autres études récentes (Drolet et al. 1999; Lichstein et al. 2002a; 2002b) qui ont détecté une agrégation spatiale des territoires d'oiseaux forestiers, même après avoir tenu compte de la végétation. Cependant, les espèces ayant le plus tendance à regrouper les territoires n'était pas les plus sensibles à la structure des forêts. La tendance à regrouper les territoires ne pouvait donc pas être utilisée pour prédire l'association aux habitats de grande superficie dans mon aire d'étude. Par contre, mes résultats suggèrent que la présence des individus conspécifiques joue un rôle important lors de la colonisation des territoires de nidification chez la plupart des espèces de passereaux forestiers.

La Paruline couronnée (*Seiurus aurocapilla*) est une espèce territoriale et sensible à la structure des forêts (Van Horn et Donovan 1994; Ortega et Capen 1999; Porneluzi et Faaborg 1999; Bayne et Hobson 2002). Dans le contexte de la perte et de la fragmentation des forêts, la Paruline couronnée est l'une des espèces de passereaux forestiers les plus étudiées. Par contre, jusqu'à présent, les évènements survenant avant la colonisation de l'habitat ont rarement été mesurés. Au troisième chapitre de ma thèse, les territoires de Paruline couronnée étaient significativement agrégés, même après avoir tenu compte de la répartition spatiale de la végétation locale. Ce résultat suggère que les individus pourraient avoir tendance à installer leur territoire de nidification à proximité de ceux d’individus conspécifiques. J’ai donc vérifié si la présence des voisins conspécifiques influençait la colonisation des territoires de nidification par les mâles et les femelles. J’ai montré dans le quatrième chapitre que la présence et le nombre de voisins conspécifiques n’incitaient pas les mâles à remplacer des territoires vacants. Par contre, les analyses de mon cinquième chapitre montrent que les femelles étaient plus présentes dans les populations avec de fortes densités de mâles territoriaux. Les études antérieures avaient principalement expliqué la répartition des femelles en fonction du degré de fragmentation de la forêt (Porneluzi et Faaborg 1999; Burke et Nol 2000; Bayne et Hobson 2001; Bourque et Villard 2001). Mes résultats suggèrent plutôt que la fragmentation des forêts influence indirectement la répartition des femelles en empêchant le regroupement des territoires des mâles. De ce fait, les densités de mâles sont plus faibles en milieu fragmenté, ce qui rendrait les mâles de ces milieux moins attirants pour les femelles.

Principales retombées de l’étude et avenues de recherche

Cette thèse était motivée par la recherche de principes généraux pour expliquer la répartition des populations aviaires. Je montre que les espèces de passereaux forestiers diffèrent entre elles par rapport à leur facilité à se déplacer en milieu ouvert. De plus, la tendance à regrouper les territoires varie entre les espèces. Par contre, les différences observées entre les espèces ne permettaient pas de prédire leur sensibilité à la structure des forêts. La variation importante de mes estimations ainsi que le faible nombre d’espèces qui pouvaient être étudiées sont des facteurs qui ont probablement contribué à la faible puissance de mes analyses. Cependant, même si beaucoup plus d’espèces pouvaient être étudiées, l’emplacement des points dans mes analyses suggère qu’aucune relation n’apparaîtrait. Les conclusions de grande portée pouvant expliquer la répartition des espèces restent donc élusives. Mais la recherche sur les principes généraux gouvernant la répartion des espèces mérite d’être poursuivie puisque la découverte de tels principes aurait une grande valeur pour la gestion des populations. De plus, la recherche sur les comparaisons interspécifiques doit être combinée avec des mesures de conservation. Par exemple, je montre dans cette thèse que les femelles de la Paruline couronnée sont attirées par les populations avec de fortes densités de mâles territoriaux, indépendamment de la quantité de forêt dans les paysages. Il faudrait déterminer si c’est le cas chez d’autres espèces forestières qui montrent un succès d’appariement plus faible dans les paysages avec un faible couvert forestier. Advenant une réaction similaire des femelles d’autres espèces à la densité des mâles, il faudrait s’assurer de maintenir des parcelles de forêt de grandes superficies dans les paysages. La conservation de telles parcelles pourraient être nécessaire à l’établissement de populations de fortes densités, ce qui amènerait indirectement un meilleur succès d’appariement des mâles et contribuerait à maintenir la viabilité des populations.

Dans mon aire d’étude, les superficies boisées ont été durement touchées par le déboisement au cours des dernières années (MRNQ 2004). En effet, depuis 2002, les exploitations porcines existantes doivent disposer de superficies cultivées pour l’épandage des fumiers (MRNQ 2004). De plus, les nouveaux exploitants d’élevage porcin doivent disposer, en propriété, d’au moins 50 % des superficies nécessaires pour l’épandage de déjections de leurs animaux (MRNQ 2004). En conséquence, le défrichage des boisés a été accéléré pour permettre l’épandage du fumier. Les espèces réticentes à traverser les milieux ouverts et celles qui regroupent leurs territoires pourraient être négativement affectées par cette perte d’habitat et ce changement de configuration des boisés. On pourrait donc s’attendre à une diminution des effectifs des populations de ces espèces dans l’aire d’étude.

La recherche sur l'influence de la structure du paysage sur les oiseaux est imposante et diversifiée (Fahrig 2003). Cependant, différents chercheurs mesurent la structure du paysage avec différentes variables et à différentes échelles. Or, plusieurs des variables utilisées pour mesurer la structure du paysage ont rarement été validées (Hargis et al. 1998; McAlpine et Eyre 2002). De plus, le choix de l'échelle spatiale peut affecter directement les résultats d'une étude (Mayer et Cameron 2003). Dans ma thèse, j'ai mesuré la structure du paysage à l'aide de variables considérées standards. Par contre, ces variables sont probablement plus efficaces pour les paysages contenant des fragments de forêts isolés plutôt que pour les paysages dont les parcelles sont reliées entre elles. En effet, de nombreuses études ont analysé la relation entre la démographie des oiseaux et des variables telles que la superficie des parcelles ou encore la proximité entre les parcelles (e.g. Robinson et al. 1995; Donovan et al. 1997; Boulinier et al. 2001). De telles variables peuvent être quantifiées seulement lorsque les parcelles de forêt sont isolées et bien définies. Il s'ensuit que de futures études devraient identifier les variables qui définissent le mieux la structure des paysages lorsque les parcelles sont agrégées. Éventuellement, il serait également utile de tenter d'évaluer l'échelle spatiale la plus efficace pour quantifier la sensibilité à la structure des forêts des passereaux forestiers. Dans ma thèse, l'utilisation de différentes échelles spatiales pour mesurer l'occurrence des espèces et/ou la structure des paysages a modifié l'ordre de sensibilité à la structure des forêts des espèces étudiées. Ce résultat suggère que les comparaisons interspécifiques seront plus robustes lorsque les échelles spatiales appropriées seront déterminées.

Cette thèse s'inscrit dans le cadre des études qui cherchent à comprendre la sensibilité à la structure des forêts plutôt qu'à simplement énumérer la sensibilité de différentes espèces. De nombreux auteurs débattent présentement sur la meilleure façon de contrer la perte et la fragmentation des forêts (voir Beier et Noss 1998; Lichstein et al. 2002a; Gram et al. 2003;

Mayer and Cameron 2003; Stephens et al. 2004). L’existence même de ce débat après des dizaines d’années de recherche indique qu’il importe d’identifier les principes généraux qui influencent la répartition des espèces, et ce, dans le but de guider la prise de décision par les gestionnaires. Les travaux de ma thèse sur les comportements qui pourraient influencer la répartition des individus méritent donc d’être repris dans d’autres régions et avec d’autres espèces. Les résultats de ces futures recherches permettront de préciser la contribution des comparaisons interspécifiques pour l’établissement de principes généraux. En effet, il importe d’aller au-delà de la simple énumération du degré de sensibilité des espèces. La suite logique implique l’étude de facteurs potentiels (végétation locale, mouvements, information publique, etc.) et de lier quantitativement les réponses entre les espèces avec l’approche comparative.

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