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**STRUCTURE DU PAYSAGE
ET ÉCOLOGIE COMPORTEMENTALE
DES OISEAUX FORESTIERS EN HIVER**

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Résumé

Les effets de la déforestation sur les effectifs des populations d'oiseaux ont fait l'objet de nombreuses études au cours des dernières décennies. Cependant, relativement peu d'entre elles ont été réalisées en dehors de la période de reproduction. Mon projet de recherche avait pour objectifs de décrire les effets de la déforestation sur les populations d'oiseaux forestiers dans un contexte hivernal et de mettre en évidence, à l'aide d'une approche expérimentale, d'éventuels mécanismes comportementaux pouvant affecter la dynamique des populations étudiées et leur répartition spatiale. Les travaux d'échantillonnage sur le terrain ont eu lieu pendant trois hivers au Kamouraska. La structure de 24 paysages (rayon de 500 m) a été décrite à partir d'une image satellite. Ces paysages représentaient un gradient complet de déforestation (8 à 88% de couvert forestier). Dans la moitié de ces paysages, de la nourriture a été fournie *ad libitum* pendant tout l'hiver. L'intégrité des peuplements forestiers (une composante principale incorporant les variables couvert forestier et densité des bordures) était positivement associée à l'abondance des Mésanges à tête noire et à la richesse spécifique pendant l'expérience d'approvisionnement en nourriture mais, seulement dans les paysages expérimentaux. Dans les paysages témoins, l'abondance des Mésanges à tête noire et la richesse spécifique ont au contraire légèrement diminué avec une augmentation de la valeur de l'intégrité des peuplements forestiers. Ces résultats suggèrent que les paysages témoins où la déforestation n'était pas marquée ont pu faciliter l'émigration d'oiseaux lorsque les conditions environnementales (froid, rendement énergétique lors de la quête alimentaire) se sont détériorées. En contrepartie, dans les paysages témoins où la déforestation était sévère, des oiseaux ont pu se trouver piégés. Néanmoins, la structure des paysages n'avait aucun effet sur la condition énergétique des mésanges. Seul l'approvisionnement en nourriture a eu un effet positif sur la condition des mésanges mais aussi, sur leur patron quotidien d'engraissement. Finalement, les mésanges des paysages témoins les plus sévèrement déboisés avaient une plus grande propension à s'exposer en milieu ouvert à d'éventuels prédateurs, tandis que celles bénéficiant de l'approvisionnement en nourriture demeuraient toujours en retrait, à proximité du couvert forestier.

Abstract

Over the last few decades, many researchers have addressed the impacts of forest loss on forest bird abundance. However, most of these works were conducted during the breeding season. The aim of my research was to document the effects of deforestation on bird populations during winter. Using an experimental approach, I also wanted to assess the effect of behavioral mechanisms potentially affecting population dynamics and spatial distribution of forest birds. Field work was conducted during three winters in Kamouraska County. The structure of 24 landscapes (500-m radius) was described from a satellite image. These landscapes represented a broad gradient of deforestation (forest cover 8–88 %). In half of these landscapes, we provided an unlimited source of food. I evaluated the effects of landscape structure 1) on the spatial distribution of the forest bird community, 2) on the fattening strategies, and 3) the anti-predator behavior of the Black-capped Chickadee (*Poecile atricapillus*). Forest integrity (a composite of forest cover and edge density) was positively associated with chickadee abundance and species richness in landscapes that were supplemented. However, in control landscapes, chickadee abundance and species richness tended to decrease with an increase in forest integrity. This suggests that the more forested control landscapes facilitated winter emigration when conditions deteriorated. Conversely in highly deforested and fragmented control landscapes, birds became “gap-locked”. Landscape structure did not affect chickadees’ energetic condition. However, food-supplementation improved it and affected the pattern of daily fattening as well. In the more deforested control landscapes, chickadees showed more willingness and ventured farther into the open despite a likely increase in the risk of predation. However, where *ad libitum* food was available prior to the experiment, chickadees always remained close to the forest edge, regardless of the level of deforestation.

Avant-Propos

Afin de pouvoir mener à terme ce projet de recherche, j'ai pu compter sur la collaboration d'un grand nombre de personnes. Je suis tout d'abord extrêmement reconnaissant envers Christine Pomerleau, Maude Pelletier, Valérie Godbout, Caroline Fournier, Florence Portal et Lluís Brotons pour toute l'aide apportée lors de la réalisation des travaux sur le terrain. Mille excuses pour vos engelures! L'expertise de Bruno Drolet lors de l'analyse de l'image satellite de l'aire d'étude et de la réalisation des cartes s'est avérée des plus utiles. Bruno, t'es un Michel-Ange de la géomatique!

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Introduction

Déforestation et déclin des populations d'oiseaux

Les effets de la perte des habitats forestiers sur la faune et ce, tant chez les invertébrés que chez les vertébrés, ont fait l'objet d'un nombre considérable d'études au cours des quelque 25 dernières années (Hanski 1994, Pimm 1998, Kolozsvary et Swihart 1999). Les études portant plus spécifiquement sur les impacts perceptibles au niveau des effectifs des populations d'oiseaux ont été particulièrement nombreuses mais aussi, parmi les plus médiatisées (Terborgh 1989). Ainsi, de nombreux chercheurs ont-ils démontré les effets négatifs de la dégradation des habitats forestiers sur l'abondance (Lee et al. 2002, Schmiegelow et Mönkkönen 2002), la richesse spécifique (Freemark et Merriam 1986, Villard et al. 1999, Boulinier et al. 2001) et la persistance des populations au fil des ans (Aberg et al. 2000, Hames et al. 2001).

Causes présumées du déclin des populations

Au cours des dernières décennies, des tendances à la baisse ont été constatées dans les effectifs de certaines populations d'oiseaux forestiers telles que, la Grive des bois (*Hylocichla mustelina*), le Pioui de l'Est (*Contopus virens*) ou encore, la Paruline à poitrine baie (*Dendroica castanea*) (Robbins et al. 1989, Downes et Collins 2003). Le débat portant sur la nature exacte des causes à l'origine de tels déclin se poursuit toujours (Fahrig 1997, Harrison et Bruna 1999, Flather et Bevers 2002, Haila 2002). Néanmoins à ce jour, plusieurs mécanismes au-delà de la simple perte d'habitat, ont pu être mis en évidence afin d'expliquer les effets négatifs de la déforestation sur l'abondance des oiseaux forestiers et leur répartition spatiale. La majorité des mécanismes identifiés ont cours à l'intérieur des habitats boisés eux-mêmes et ce, particulièrement à proximité des bordures. Ainsi il a été démontré qu'à proximité des bordures, en raison de l'humidité moins élevée du sol, certains groupes d'insectes forestiers dont s'alimentent les oiseaux peuvent être moins abondants (Burke et Nol 1998, Zquette et al. 2000, Van Wilgenburg et al. 2001). L'incidence de la prédation des couvées par des serpents, des oiseaux tel que le Geai bleu (*Cyanocitta cristata*) et des mammifères tel que l'Écureuil roux (*Tamiasciurus hudsonicus*) (Robinson

et al. 1995, Crooks et Soulé 1999, Schmidt 2003), de même que le parasitisme des nids par le Vacher à tête brune (*Molothrus ater*), y sont aussi plus marqués (Robinson et al. 1995) et ce, davantage encore à l'intérieur de matrices résultant de l'agriculture plutôt que de l'exploitation forestière (Rodewald et Yahner 2001). Certaines espèces, telle que la Paruline couronnée (*Seirus aurocapillus*), dites « d'intérieur » (*forest-interior specialists*, sensu Whitcomb et al. 1981), semblent tout simplement éviter la proximité des bordures pour établir leur territoire lors de la nidification (Hunta et al. 1999, Brand et George 2001). Dans les habitats où la déforestation est marquée au point d'entraîner la fragmentation des paysages forestiers (Andrén 1994), il va sans dire que ces effets seront d'autant plus manifestes lorsque les fragments de forêt résiduelle seront petits, non seulement parce que l'effet de la bordure se fera sentir sur une plus grande proportion de la surface boisée mais aussi, parce que certaines espèces (*area-sensitive species*, sensu Freemark et Collins 1992), telle que le Tangara écarlate (*Piranga olivacea*), n'y trouveraient pas les grandes surfaces boisées qu'elles recherchent (Austen et al. 2001).

D'autres mécanismes invoqués pour expliquer les patrons d'abondance et de distribution des oiseaux forestiers révèlent l'importance directe de la matrice (champs, bûchers, etc.) à l'intérieur de laquelle se retrouvent les habitats forestiers. Ainsi, le taux d'appariement à l'intérieur d'îlots boisés est affecté par leur degré d'isolement (Gibbs et Faaborg 1990, Villard et al. 1993), les habitats fortement fragmentés réduisant de manière importante la mobilité des individus (Bélisle et al. 2001, Graham 2001, Gobeil et Villard 2002). Ce type de résultats a amené la formulation du concept de perméabilité du paysage aux déplacements des individus (*landscape connectivity*, sensu Taylor et al. 1993). De plus, il a été démontré que les individus qui s'aventurent plus loin à l'intérieur des ouvertures séparant les fragments de forêts sont plus fréquemment victimes des prédateurs aériens (Hinsley et al. 1995).

Le contexte hivernal

La plupart des mécanismes mentionnés plus haut ont été mis en évidence au cours d'études portant sur des espèces en période de reproduction. Qu'en est-il des mécanismes ayant un impact sur la dynamique des populations d'oiseaux pendant l'hiver? L'hiver représente un

véritable défi pour les oiseaux forestiers des écosystèmes nordiques en ce qui a trait à la gestion de leurs réserves énergétiques et donc ultimement, à leur survie (Graber et Graber 1979, Perkins et al. 1997). Pendant l'hiver, les températures froides rendent nécessaire la consommation d'une importante quantité de nourriture. Paradoxalement, l'abondance de la nourriture se trouve alors à son niveau annuel le plus bas, du moins celle d'origine animale (insectes, araignées, etc.). De plus, cette situation ne fait guère qu'empirer tout au long d'une période s'étendant de la fin de l'automne au début du printemps, la quantité de nourriture disponible ne cessant de diminuer au cours de cette période (soit pendant environ 6 mois à notre latitude). Ce contexte de crise énergétique se trouve exacerbé par le fait qu'en cette période de l'année, la durée des jours étant grandement réduite, les oiseaux disposent alors de relativement peu de temps afin de combler leurs besoins énergétiques courants et pour constituer les réserves endogènes qui leur permettront de survivre au jeûne nocturne.

Afin de pouvoir maintenir leur équilibre énergétique et survivre dans un tel contexte environnemental, les espèces résidentes des milieux nordiques ont développé de remarquables adaptations. Certaines de celles-ci sont comportementales telles que la constitution de caches de nourriture (Kallander et Smith 1990), la sélection, lors de la quête alimentaire, de sites exposés au soleil (Carrascal et al. 2001) ou à l'abri du vent (Grubb 1977), la formation de petits groupes compacts (Heinrich 2003) ou l'utilisation de cavités pendant la nuit (Cooper 1999), les deux dernières adaptations contribuant à réduire de manière importante les pertes de chaleur par radiation et par convection (Walsberg 1986).

Les adaptations de nature physiologique sont également nombreuses. Celles-ci comprennent une augmentation de la densité du plumage (Middleton 1986), une augmentation du métabolisme basal (Broggi et al. 2004), une augmentation de la capacité thermogénique (Cooper et Swanson 1994), une augmentation de l'endurance thermogénique (Swanson 1990), une augmentation de la tolérance au froid (Liknes et al. 2002), une diminution de la conductance thermique (Cooper et Gessaman 2004), l'hypothermie nocturne facultative (McKechnie et Lovegrove 2002) et finalement, l'accumulation saisonnière et journalière de réserves lipidiques (Pravosudov et Grubb

1997a), les acides gras étant le principal substrat utilisé lors de la thermogénèse (Carey et Dawson 1999).

Un constat s'impose. Malgré l'importance de l'hiver dans le cycle biologique annuel des d'oiseaux résidants et l'intérêt académique que représente l'étude des phénomènes spécifiques à cette saison, beaucoup moins de chercheurs se sont intéressés à ce jour aux effets de la fragmentation des habitats sur l'écologie des espèces résidentes des écosystèmes tempérés et nordiques, en dehors de la saison de reproduction. Conséquemment, notre connaissance des effets de la déforestation sur l'abondance, la répartition spatiale et, notre compréhension des mécanismes affectant la dynamique des populations d'oiseaux des paysages partiellement déboisés pendant l'hiver sont-elle encore relativement fragmentaires.

Structure de la thèse

La présente étude porte sur les effets de la déforestation sur l'abondance, la répartition spatiale et les décisions comportementales des oiseaux forestiers pendant l'hiver. Les travaux d'échantillonnage sur le terrain ont été réalisés pendant trois hivers au Kamouraska, dans un paysage agro-forestier présentant un gradient complet de déforestation. Certains aspects des travaux ont porté sur toutes les espèces d'oiseaux présentes dans les habitats étudiés. Cependant, la majeure partie des efforts a été consacrée à l'étude intensive de certains aspects de l'écologie de la Mésange à tête noire (*Poecile atricapillus*). Cette espèce n'a pas été choisie pour des raisons de vulnérabilité face à la déforestation ou d'un quelconque statut d'espèce menacée. Bien au contraire, c'est essentiellement en raison de son abondance et de sa relative ubiquité qu'elle a été choisie comme espèce modèle, du moins pour la guildes des oiseaux s'alimentant dans les arbres, facilitant ainsi la vérification de mes hypothèses de recherche. Il aurait en effet été beaucoup plus difficile, du moins beaucoup plus coûteux, d'entreprendre une telle étude sur une espèce moins abondante comme la Sittelle à poitrine rousse (*Sitta canadensis*) ou encore, le Grand Pic (*Dryocopus pileatus*).

Je me suis tout d'abord intéressé aux effets de la structure du paysage forestier sur l'abondance et la répartition spatiale des oiseaux à la fin de l'automne et, au cœur de

l'hiver. Le cœur de l'hiver représente une période de l'année où, en raison de la demande énergétique élevée imposée par les conditions climatiques, la quantité de nourriture disponible risque de représenter éventuellement, parce que non renouvelable, un facteur limitant les populations. J'ai donc voulu vérifier expérimentalement si un apport d'énergie alimentaire illimitée pouvait modifier l'abondance et la répartition spatiale des oiseaux et ce, à l'intérieur d'un gradient complet de déforestation. Les résultats obtenus et les interprétations en découlant sont présentés dans le premier chapitre intitulé « *Landscape-dependent distribution of northern forest birds during winter* ». Ce premier volet de l'étude a nécessité l'inventaire des communautés d'oiseaux présentes dans les habitats étudiés. La réalisation de tels inventaires en dehors de la période de reproduction est problématique puisque les oiseaux, contrairement à la situation prévalant au début de l'été, sont beaucoup plus silencieux et se déplacent alors sur des surfaces beaucoup plus grandes que ne le sont leurs territoires de nidification. J'ai donc eu recours pendant les inventaires à la diffusion d'un enregistrement de cris de houspillage de la Mésange à tête noire, afin d'augmenter la probabilité de détection des oiseaux présents dans les paysages étudiés. Les cris de houspillage de la Mésange à tête noire sont en effet réputés pour le pouvoir d'attraction qu'ils exercent non seulement sur les membres de cette espèce mais aussi, sur plusieurs autres espèces d'oiseaux forestiers (Hurd 1996). Cette méthodologie est décrite à l'Annexe A intitulée « *Playbacks of mobbing calls of Black-capped Chickadees help estimate the abundance of forest birds in winter* ».

La répartition spatiale des populations nous renseigne, du moins partiellement, sur la qualité des habitats. Cependant, qu'en est-il de la condition énergétique des individus malgré tout présents dans les habitats qui pourraient être présumés de moindre qualité? Les habitats forestiers fragmentés sont considérés plus coûteux d'un point de vue énergétique (Hinsley 2000). Je me suis donc à nouveau intéressé aux effets de la structure du paysage forestier mais cette fois, sur la condition énergétique des Mésanges à tête noire à la fin de l'automne et, au cœur de l'hiver. J'ai voulu vérifier expérimentalement et ce, toujours à l'intérieur du même gradient complet de déforestation, si un apport d'énergie alimentaire illimitée pouvait avoir un effet sur leur condition énergétique mais aussi, s'il pouvait modifier leur patron journalier d'engraissement des oiseaux présents. Le deuxième chapitre

intitulé « *Landscape structure, food abundance and winter fattening strategies in black-capped chickadees* » présente les résultats et interprétations découlant de cette expérience.

Dans la mesure où dans les habitats de moindre qualité, la condition énergétique des Mésanges à tête noire serait affectée ou encore, que le gain énergétique net escompté lors de la quête alimentaire y serait moindre, j'ai voulu vérifier si au cœur de l'hiver, celles-ci seraient davantage enclines à s'exposer au risque d'être victimes de prédateurs. J'ai donc réalisé une expérience visant à évaluer la propension des oiseaux à s'exposer en milieu ouvert aux prédateurs, dépendamment à nouveau de la sévérité du déboisement et de la quantité de nourriture disponible. Cette expérience est présentée dans le troisième et dernier chapitre de la thèse intitulé « *Landscape-dependent response to predation risk by forest birds* ».

Chapitre I: Landscape-dependent distribution of northern forest birds in winter

Avertissement

Le contenu de ce chapitre a été publié en avril 2005. Hormis quelques changements mineurs dans le format ayant été nécessaires à la préparation de la thèse, le lecteur trouvera ici toute l'information contenue dans :

Turcotte, Y, and A. Desrochers. 2005. Landscape-dependent distribution of northern forest birds in winter. *Ecography* 28: 129-140.

Résumé

Nous avons évalué les effets de la structure du paysage le long d'un gradient de déforestation (couvert forestier variant de 8 à 88 % à l'intérieur d'un rayon de 500 m, $n = 24$ paysages), sur la répartition spatiale des oiseaux forestiers en hiver, dans le comté de Kamouraska, Québec. Nous avons de plus conçu une expérience visant à déterminer si d'éventuels effets persisteraient si, dans la moitié des paysages étudiés (paysages expérimentaux), une source illimitée d'énergie alimentaire (sous la forme de graines de tournesol et de gras de bœuf) devenait disponible. Nous avons analysé ces effets au niveau d'une population de Mésanges à tête noire (*Poecile atricapillus*), en considérant comme variable dépendante le nombre d'individus recensés, lors de la diffusion d'un enregistrement de leurs cris de houspillage, pendant 5 minutes, dans un rayon de 50 m. Nous avons également analysé ces effets au niveau de la communauté, en nous référant cette fois à la richesse spécifique. Lors du premier des deux hivers qu'a duré cette étude, en novembre, avant le début de l'approvisionnement en nourriture, une composante principale correspondant à l'intégrité des peuplement forestiers (incorporant les variables couvert forestier et densité des bordures) était positivement associée à l'abondance des Mésanges à tête noire et à la richesse spécifique. Au cours des deux hivers, de décembre à février, pendant l'approvisionnement en nourriture, cette composante principale était encore une fois positivement associée à l'abondance des Mésanges à tête noire et à la richesse spécifique mais, seulement dans les paysages expérimentaux. Dans les paysages témoins, l'abondance des Mésanges à tête noire et la richesse spécifique ont au contraire, légèrement diminué avec une augmentation de la valeur de cette composante principale. Nos résultats semblent indiquer que les paysages témoins où la déforestation n'était pas marquée ont pu faciliter l'émigration d'oiseaux lorsque les conditions environnementales (froid, diminution sous un certain seuil de la quantité de nourriture disponible, diminution de la période de luminosité) se sont détériorées. Conséquemment, nos résultats suggèrent également que, dans les paysages témoins où la déforestation était sévère, des oiseaux ont pu se trouver piégés lorsque les conditions climatiques rigoureuses ont amplifiées les contraintes limitant déjà leurs mouvements entre les fragments de forêts.

Abstract

We evaluated the effects of landscape structure, along a broad gradient of deforestation (forest cover 8–88 %, 500-m radius), on the spatial distribution of forest birds exposed to winter climatic conditions, in Quebec, Canada. Concurrently, we conducted an experiment to determine if these effects would persist if an unlimited source of energy, provided by food-supplementation, became available. We analyzed these effects at the population level, using count data of black-capped chickadees *Poecile atricapillus*, but also at the community level, referring to species richness. In one of the two years of the study, before food-supplementation began (November), “forest integrity” (a composite of forest cover and edge density) was positively associated with chickadee abundance and species richness. Each year, forest integrity was also positively associated with chickadee abundance and species richness in landscapes that were supplemented (December - February). However, in control landscapes, during the food-supplementation period, chickadee abundance and species richness tended to decrease with an increase in forest integrity. We argue that the more forested control landscapes facilitated winter emigration of juveniles and transient birds. Conversely, our results further suggest that, in the highly deforested and fragmented control landscapes, birds became “gap-locked” when rigorous winter climatic conditions exacerbated already existing movement constraints.

Introduction

Over the last few decades, many researchers have addressed the impacts of forest loss and, beyond some threshold, fragmentation (Andrén 1994), on forest bird abundance and species richness. Stimulated by the persisting theoretical debate about the relative importance of the ecological processes involved (reviewed by Haila 2002), many empirical studies reported positive associations of woodlot size, total forest cover or other metrics related to habitat area, with bird abundance (e.g., Lee et al. 2002), species richness (e.g., Boulinier et al. 2001) or temporal stability in populations and communities (e.g., Hames et al. 2001).

Beyond the direct effects of habitat loss, several mechanisms have been invoked to explain how changes in landscapes actually impact individuals to result in declines in population size or species richness larger than expected from habitat loss alone. Thus, processes within habitat fragments such as reduced food supply (e.g., Burke and Nol 1998), edge avoidance (e.g., Huhta et al. 1999), increased nest predation (e.g., Crooks and Soulé 1999) and nest parasitism (e.g., Robinson et al. 1995), have been invoked so far to explain the observed declines. More rarely, processes occurring in the matrix between habitat fragments have also been singled out. Thus, reduced pairing success observed in isolated forest patches has been attributed to the low connectivity (“...the degree to which the landscape facilitates or impedes movement among resource patches”; Taylor et al. 1993) allowed by severely deforested landscapes (e.g., Villard et al. 1993).

Most of these proposed mechanisms arose from works conducted during the breeding season. In fact, relatively few studies have specifically assessed the effects of deforestation on bird abundance or species richness during the non-breeding season, despite its temporal and biological importance in the annual cycle. At the higher latitudes particularly, winter represents a critical energy management challenge: sub-zero temperatures persist for several months, birds must endure long fasting at night, day length limits their time available for foraging, and food supply steadily decreases.

In this “energy crisis” context, our understanding of the processes responsible for the spatial distribution and patterns of abundance of birds, in partially deforested landscapes, remains incomplete. During winter, any changes in population size or species richness in these landscapes, suboptimal beforehand from an energetic point of view (Hinsley 2000), would have to result either from mortality, emigration or immigration. Recently, Doherty and Grubb (2002) reported positive trends between apparent winter survival of some, but not all, species of forest birds and size of small (0.54 to 6.01 ha; Doherty and Grubb 2000) isolated woodlots in Ohio. On the other hand, Matthysen (1999) studied a wider gradient of woodlot sizes and concluded that, in Belgium, yearly survival of nuthatches *Sitta europaea* was unrelated to forest size (1 to 1500 ha).

Populations build-up at feeders during winter, far above numbers that could be expected to come from the immediate surrounding habitats (e.g., Loery and Nichols 1985, Wilson 2001), irruptions (e.g., Bent 1946, Koenig and Knops 2001), and within winter long range banding recoveries, for many species not even considered migratory (e.g., Wallace 1941, Browning 1995, Brewer et al. 2000), are well documented. These phenomena illustrate the importance of emigration and immigration on forest bird population dynamics during winter. Yet, we do not know to what extent these movements are impeded by the combined effects of partially deforested landscapes and rigorous winter climatic conditions.

In this study, our objectives were 1) to evaluate the effects of landscape structure, along a complete gradient of deforestation, on the spatial distribution of forest birds exposed to severe winter climatic condition, just before, and in the heart of winter, and 2) to determine experimentally how spatial distribution would be affected if an unlimited source of food became available, thus compensating, toward one end of this gradient, for an insufficient continuous habitat area. We analyzed these potential effects at the community level, referring to species richness, and at the population level, using count data of the black-capped chickadee *Poecile atricapillus*.

Methods

Study area and experimental design

This study was conducted during the winters of 1998-1999 and 1999-2000, from mid-November through mid-February, on the south-east shore of the St. Lawrence River estuary, in Kamouraska County (47°30' N, 69°50' W), Quebec, Canada (Fig. 1). The study area covers approximately 600 km² of agricultural landscape where balsam fir *Abies balsamea*, quaking aspen *Populus tremuloides*, white spruce *Picea glauca* and paper birch *Betula papyrifera* dominate arboreal vegetation. The study area is part of the Temperate Cold ecoclimatic region (Ecoregion Working Group 1989; Fig. 1). At the La Pocatière climate station, located within the study area, daily mean temperatures (1971-2000) for November, December, January, and February are respectively, -0.1°C, -8.3 °C, -11.7 °C, and -10.3 °C (Anon. 2004).

We selected 24 circular, 500-m radius, and non-overlapping landscapes, centered on a sharp edge between a field and a forest (Fig. 1). We chose a 500-m radius in order to include the core of most home ranges of black-capped chickadee winter flocks (10 - 20 ha; reviewed by Smith 1991) that would occur at the center of the landscapes, while minimizing the inclusion of habitat beyond their normal flock range. Black-capped chickadee, our model species, is by far the most abundant permanent-resident forest bird species in the study area (Turcotte and Desrochers 2002). We established 12 pairs of adjacent landscapes with similar forest characteristics. The centers of these paired landscapes were separated from each other by 2.5 - 5 km. We chose this distance as we wanted it large enough to reduce the likelihood that some chickadees would be frequenting both landscapes over the same winter, while small enough, to guarantee environmental conditions (microclimate, wild food abundance, predation pressure) as similar as possible within each pair of landscapes, throughout the study area. Thus, we reduced the risk of unwanted confounding geographic effects.

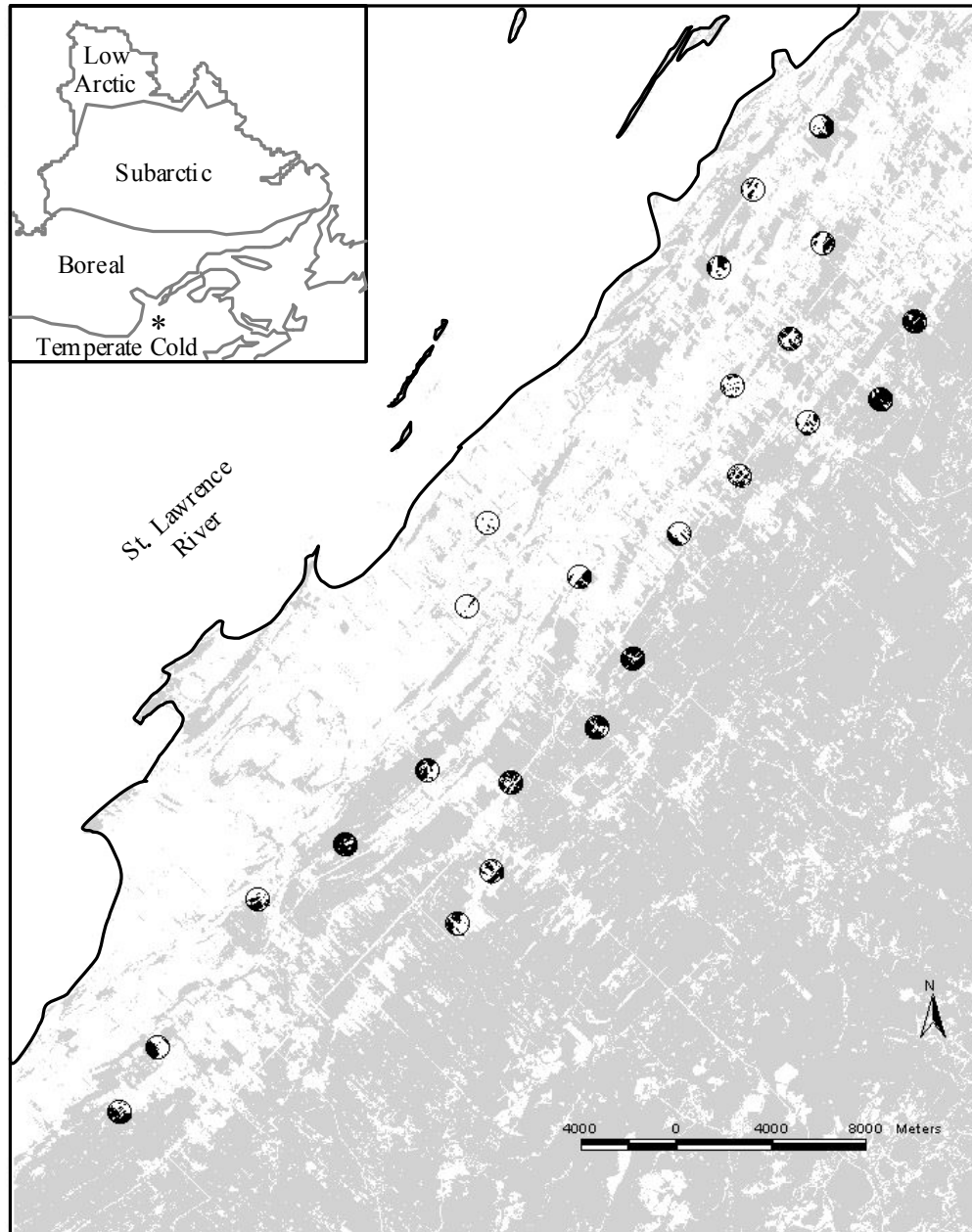


Figure 1. The study area in Kamouraska County, Quebec, Canada. Circles indicate the 24 500-m radius landscapes. Nonforest habitats are in white, forests within the 24 landscapes are in black while surrounding forests are in gray, as determined by a LANDSAT-7 satellite image taken in August 1999. In the insert, ecoclimatic regions in eastern Canada and localization (asterisk) of the study area.

We provided sunflower seeds and beef suet *ad libitum* at the center of one landscape of each pair (hereafter, supplemented landscapes; as opposed to control landscapes) from mid-November through the end of winter (hereafter, treatment period; as opposed to pre-treatment period, the first half of November before the beginning of food treatments). The same food treatments (supplementation or control) were conducted in each landscape during both winters. Habitations and other feeders than ours were present in the study area. As we wanted to reduce the likelihood that some birds using control landscape would nevertheless benefit from human food supplementation, we could not randomize the assignment of food treatments. Therefore, habitations (and possible food supplementation from other sources) were indeed present in all supplemented landscapes while the center of each control landscape was always located at least one kilometer from the nearest habitation.

Landscape characterization

To describe the structure of the 24 landscapes under study, we selected the three landscape metrics that we considered, referring to both natural history (e.g., Bent 1946) and landscape ecology (e.g., Andr en 1994, Fahrig 1997), the most likely to explain the distribution of forest birds. We chose forest cover (%) to quantify the area of potentially suitable habitats in the landscape for forest birds. Because edges have been shown to affect space use by forest birds during winter (e.g., Dolby and Grubb 1999, Brotons et al. 2001), we chose edge density (m/ha of forest) as an index of forest fragmentation. Finally, we used the proportion of conifers in the forest (%) to provide information about the nature of forested vegetation as some species may appear or disappear along this gradient (e.g., boreal chickadee *P. hudsonica* vs black-capped chickadee) and as we considered that coniferous vegetation could act as wind-breakers and compensate for the lack of protection against the wind in the more fragmented landscapes. We used Patch Analyst (Elkie et al. 1999) to obtain these landscape metrics from a LANDSAT-7 satellite image taken in August 1999. Prior to all analyses, edge density values were log transformed (hereafter, Ln edge density) while the proportion of conifers in the forest values were arcsine square-root transformed (hereafter, Asqrt conifers), in order to approximate normality.

We chose not to use popular landscape metrics such as number of forest patches, mean patch size, or mean distance to nearest patch to characterize our landscapes because most of the forest cover did not appear in patches isolated from one another. In fact, forested areas within the 500-m radii were generally in continuity with surrounding forests (Fig. 1).

Bird surveys

During winter, forest birds are less vocal and generally dwell over areas larger than their breeding territories. These factors lessen their probability of detection and would therefore severely compromise the reliability of standard point counts. Thus, we used playbacks of mobbing calls of black-capped chickadees to estimate bird abundance during point counts. The use of this type of playback during winter counts allows the detection of more species and more individuals (all species combined) than standard point counts (Turcotte and Desrochers 2002). Furthermore, at least at our latitude (day length at winter solstice is 8 h 28 min; La Pocatière climate station, *unpublished data*), count results are unaffected by time of day, whether the number of individuals or species richness are considered (Turcotte and Desrochers 2002).

We conducted bird surveys at different times of day from sunrise to sunset, once per month from November through February, at the center of each of the 24 landscapes during both winters. November surveys were conducted during the pre-treatment period. In November, migrating forest bird species have already left the study area. None of them return before March. Calls were played back during 5 min with a 5-W amplifier facing skyward and placed on the ground. Sound level measured one meter above the amplifier with a sound level meter (RealisticTM) was 105 decibels. We noted all birds seen or heard within a fixed radius of 50 m. The number of birds we recorded is an index of abundance and should not be considered otherwise. We did not consider birds flying above the forest canopy as it was impossible to know if they were users of the landscapes being surveyed. Censuses were not conducted during heavy precipitation or strong wind.

Additionally, chickadees were captured with mist nets at the center of each of the 24 landscapes in November of both winters, to provide an estimation of the proportion of juveniles in our study area at the start of each winter. In November, we still were able to

age (juvenile or adult) chickadees by the amount of wear on their outermost rectrices (Pyle 1997).

Statistical methods

Forest cover and edge density are strongly associated landscape metrics (e.g. Bélisle et al. 2001). Discriminating their respective effects is sometimes practically impossible. Therefore, we used our three landscape metrics to perform a principal component analysis (PCA) with Varimax rotation. By doing so, we hoped to obtain a principal component, or factor, which would amalgamate the information provided by forest cover and Ln edge density.

Because data were counts (with variance proportional to mean), we used Poisson regressions to analyze models including the principal components describing landscapes and food treatment, as predictor variables, and black-capped chickadee abundance or species richness as response variables. We ran distinct analyses for pre-treatment and treatment periods. During treatment periods, as each landscape was surveyed once per month from December through February, count data were averaged to avoid pseudoreplication (Hurlbert 1984). We carried out statistical analyses with SAS 8.1 (Anon. 1999).

We used an information-theoretic approach (see Burnham and Anderson 2002) for the interpretation of regression results. We first relied on the coefficient of determination (R^2) to evaluate global model fit. We used this statistic as an indication of whether any of the models within a set, despite noise and randomness, could represent an acceptable approximation to an “unknown reality or truth” (Burnham and Anderson 2001). We turned afterward to the number of estimable parameters (K_i), quasi-likelihood second-order modification of the Akaike’s information criterion ($QAIC_c$), information criterion difference (Δ_i), and Akaike weight (w_i), to assess the strength of evidence supporting each of these models. Finally, in order to evaluate the relative importance of the predictor variables considered, we referred to parameter estimates and unconditional standard errors obtained by multimodel inference.

Results

Landscape structure

The 24 landscapes provided a broad gradient of forest cover (8–88 %), proportion of conifers in the forest (3–66 %), and edge density (65–796 m/ha) (for additional details, see Turcotte and Desrochers 2003). Landscape metrics within 500-m radii were strongly correlated with those describing the surrounding landscape, between 500 and 2000 m, a 15 times larger area (forest cover, $r = 0.76$, $p < 0.0001$; Ln edge density, $r = 0.65$, $p < 0.001$; Asqrt conifers, $r = 0.75$, $p < 0.0001$, $n = 24$). Thus, the 500-m radius landscapes could be considered representative of neighboring habitats, which the birds under study, had likely been using at various degrees. Asqrt conifers was neither correlated with forest cover ($r = -0.004$, $p = 0.99$, $n = 24$) nor with Ln edge density ($r = -0.05$, $p = 0.8$, $n = 24$). However, as expected, forest cover and Ln edge density values were strongly and linearly associated ($r = -0.91$, $p < 0.0001$, $n = 24$; Fig. 2).

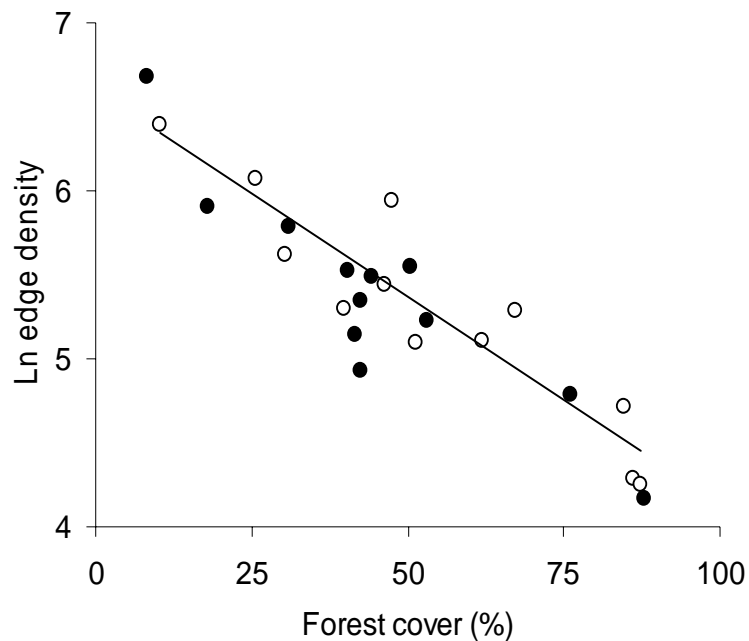


Figure 2. Relationship between forest cover (%) and Ln edge density within a 500-m radius for the 12 supplemented (filled circles) and the 12 control (open circles) landscapes.

Principal component analysis

The first principal component (PC1) explained 64% of the variance in the original landscape metrics data (Table 1). PC1 showed a high positive factor loading for forest cover and a corresponding high negative factor loading for Ln edge density. We thus interpret PC1 as a factor not only describing the amount of forested habitat in our landscapes, but also taking into account their level of fragmentation (hereafter, PC1-Forest integrity). Thus, while landscapes with the highest and lowest PC1- Forest integrity scores were, respectively, those with maximal forest cover/minimal edge density values and minimal forest cover/maximal edge density values, the effect of the level of fragmentation *per se* was obviously important in the computation of these scores (e.g. landscape 3C, forest cover = 48 %, edge density = 379 m/ha, PC1 score = -0.50; landscape 6E, forest cover = 43 %, edge density = 139 m/ha, PC1 score = 0.19).

Table 1. Landscape metric factor loadings and variance explained by the two principal components (PC1 and PC2) for the 24 landscapes.

Landscape metric	PC1	PC2
Forest cover	0.98	-0.02
Ln edge density	-0.98	-0.04
Asqrt conifers	0.01	1.00
Proportion of variance explained	0.64	0.33

A second principal component (PC2) accounted for an additional 33% of the variance (Table 1). As it had a high coefficient, positive, for Asqrt conifers alone, the interpretation of this factor is straightforward (hereafter, PC2-Conifers). Thus, PC2- Conifers scores varied accordingly with Asqrt conifers values, from the less coniferous landscape to the more coniferous landscape.

Landscape structure and use by birds

The proximity of habitations in supplemented landscapes could have affected the distribution and abundance of some species even before we began food treatments. However, during pre-treatment periods of both winters, we found no difference between control landscapes and landscapes that would become supplemented, whether we considered chickadee numbers (winter 1998-1999, control landscapes, mean = 6.5, SE = 1.2, supplemented landscapes, mean = 6.9, SE = 1.4, Wilcoxon two-sampled test, two-tailed, $S = 144$, $p = 0.7$, $n = 24$; winter 1999-2000, control landscapes, mean = 2.3, SE = 0.6, supplemented landscapes, mean = 2.7, SE = 0.5, $S = 142$, $p = 0.7$, $n = 24$) or species richness (winter 1998-1999, control landscapes, mean = 1.7, SE = 0.3, supplemented landscapes, mean = 1.6, SE = 0.3, $S = 153$, $p = 0.9$, $n = 24$; winter 1999-2000, control landscapes, mean = 0.9, SE = 0.2, supplemented landscapes, mean = 1.3, SE = 0.2, $S = 131$, $p = 0.3$, $n = 24$).

Furthermore, since counts were conducted near feeders during treatment periods in supplemented landscapes, the probability of bird detection might have been enhanced. However, our main objective was not to evaluate the effect of supplementation per se on forest birds but rather, to determine the effects of landscape structure, and its interaction with supplementation, on their response. Therefore, we need only to assume that the sampling bias due to feeders was constant across landscape types.

Playback counts allowed us to detect a total of 18 bird species during the two winters of this study (Table 2). Of these, seven occurred in at least one third of the 24 landscapes but only the black-capped chickadee was observed at least once in each landscape (Table 2).

Table 2. Number of landscapes (out of the 24 of this study) where each species was detected (two winters combined), depending on the type of landscape.

Species	Type of landscape		Total
	Control	Supplemented	
Black-capped chickadee <i>Poecile atricapillus</i>	12	12	24
Common redpoll <i>Carduelis flammea</i>	3	11	14
Downy woodpecker <i>Picoides pubescens</i>	4	8	12
Boreal chickadee <i>Poecile hudsonica</i>	3	7	10
Golden-crowned kinglet <i>Regulus satrapa</i>	5	5	10
Hairy woodpecker <i>Picoides villosus</i>	1	7	8
Blue jay <i>Cyanocitta cristata</i>	2	6	8
Red-breasted nuthatch <i>Sitta canadensis</i>	1	6	7
American goldfinch <i>Carduelis tristis</i>	1	4	5
Pine siskin <i>Carduelis pinus</i>	2	2	4
Pine grosbeak <i>Pinicola enucleator</i>	2	1	3
Gray jay <i>Perisoreus canadensis</i>	0	2	2
White-breasted nuthatch <i>Sitta carolinensis</i>	0	2	2
Brown creeper <i>Certhia americana</i>	0	1	1
Northern shrike <i>Lanius excubitor</i>	0	1	1
Evening grosbeak <i>Coccothraustes vespertinus</i>	0	1	1
Hoary redpoll <i>Carduelis hornemanni</i>	0	1	1
White-winged crossbill <i>Loxia leucoptera</i>	1	0	1

In November, chickadee numbers and population age structure differed markedly between the two winters of the study (Table 3). November species richness also showed some

differences between the two winters of the study (winter 1998-1999, mean = 1.6, SE = 0.2, winter 1999-2000, mean = 1.1, SE = 0.1, Wilcoxon signed-ranks test, two-tailed, $S = 28$, $p = 0.08$, $n = 24$). Thus, we conducted separate analyses for each winter. Due to our limited sample size, the inclusion in our models of year as a main effect, and associated interactions, would have otherwise resulted in unreliable parameter estimates (Burnham and Anderson 2002).

Table 3. Mean number of black-capped chickadees detected during playback counts and total number captured by age. Data obtained at the center of the 24 landscapes in November for the two winters of the study.

Winter	Individuals detected*			Individuals captured [†]			
	<i>n</i>	Mean	(SE)	Juveniles	(%)	Adults	(%)
1998-1999	24	6.7	(0.9)	51	(61)	33	(39)
1999-2000 ⁺	24	2.5	(0.4)	48	(22)	172	(78)

*Wilcoxon signed-ranks test, two-tailed, $S = 102$, $p = 0.0002$.

[†]Chi-square test, $X^2 = 41.9$, 1 DF, $p < 0.0001$.

⁺ A larger effort was devoted to capture during the second winter.

In the winter of 1998-1999 during the pre-treatment period, models incorporating only the predictor variable PC1-Forest integrity were the best to predict chickadee abundance (Table 4) or species richness (Table 5). Accordingly, only PC1-Forest integrity was positively associated with the number of chickadees detected (Table 6, Fig. 3) or species richness (Table 7, Fig. 4). However, in the winter of 1999-2000 during the pre-treatment period, maybe because of the low general abundance of birds at that time, global model fits were poor and we thus concluded that none of the models within a subset could be considered good enough, in some absolute sense, to predict either chickadee abundance (Table 4) or species richness (Table 5). The positive effects of PC1-Forest integrity observed during the first winter were no longer evident, either for chickadee abundance (Table 6, Fig. 3) or

species richness (Table 7, Fig. 4). However, an absence of black-capped chickadee or any other species was still more likely in landscapes with low PC1-Forest integrity values.

During treatment periods of both winters, the best models were always those with food treatment, PC1-Forest integrity and their interaction as predictor variables, to predict both chickadee abundance (Table 4) and species richness (Table 5). Surprisingly, PC1-Forest integrity had different effects in supplemented and control landscapes, on the abundance of chickadees (Table 6, Fig. 3) or species richness (Table 7, Fig. 4). Thus, an increase in PC1-Forest integrity was positively associated with abundance of chickadees or species richness only in supplemented landscapes while in control landscapes, decreasing trends, though small, in these response variables were noticeable in both winters. Consequently, chickadee numbers or species richness in supplemented and control landscapes became increasingly divergent with an increase in PC1-Forest integrity. Our limited sample size precluded a month per month (December through February) longitudinal analysis of count data (Stokes et al. 2000). However, it is worth mentioning that the slope of a linear relationship between PC1-Forest integrity and chickadee abundance or species richness in the 12 control landscapes became, and remained, negative in January during the first winter of the study, and as early as December during the second winter.

Table 4. Comparison of Poisson regression models for the association between landscape structure (PC1-Forest integrity, PC2-Proportion of conifers), food treatment (FT; supplementation or control) and the number of black-capped chickadees detected during playback counts. Data obtained at the center of the 24 landscapes during pre-treatment (November) and treatment (December - February) periods for the two winters of the study. Notation for the information-theoretic approach follows Burnham and Anderson (2002).

Winter	Period	Predictor variables	R^2	K_i^a	$QAIC_c$	Δ_i	w_i
1998-1999	Pre-treatment	PC1, PC2	0.24	4	-98.1	2.3	0.23
		PC1		3	-100.4	0.0	0.72
		PC2		3	-95.2	5.2	0.05
	Treatment	FT, PC1, PC2, FT x PC1, FT x PC2	0.52	7	-37.8	7.0	0.03
		FT, PC1, FT x PC1		5	-44.8	0.0	0.94
		FT, PC2, FT x PC2		5	-38.3	6.6	0.04

Table 4 continued.

Winter	Period	Predictor variables	R^2	K_i^a	$QAIC_c$	Δ_i	w_i
1999-2000	Pre-treatment	PC1, PC2	0.13	4	12.9	2.0	0.22
		PC1		3	13.2	2.3	0.19
		PC2		3	10.9	0.0	0.59
	Treatment	FT, PC1, PC2, FT x PC1, FT x PC2	0.73	7	-165.4	6.1	0.04
		FT, PC1, FT x PC1		5	-171.4	0.0	0.91
		FT, PC2, FT x PC2		5	-165.4	6.0	0.04

a Number of parameter for each model includes the intercept and the estimation from the global model of the variance inflation factor (*c*).

Table 5. Comparison of Poisson regression models for the association between landscape structure (PC1-Forest integrity, PC2-Proportion of conifers), food treatment (FT; supplementation or control) and species richness during playback counts. Data obtained at the center of the 24 landscapes during pre-treatment (November) and treatment (December - February) periods for the two winters of the study. Notation for the information-theoretic approach follows Burnham and Anderson (2002).

Winter	Period	Predictor variables	R^2	K_i^a	$QAIC_c$	Δ_i	w_i
1998-1999	Pre-treatment	PC1, PC2	0.24	4	46.1	2.7	0.18
		PC1		3	43.4	0.0	0.71
		PC2		3	47.2	3.8	0.11
	Treatment	FT, PC1, PC2, FT x PC1, FT x PC2	0.59	7	57.8	7.2	0.02
		FT, PC1, FT x PC1		5	50.5	0.0	0.66
		FT, PC2, FT x PC2		5	52.0	1.4	0.32

Table 5 continued.

Winter	Period	Predictor variables	R^2	K_i^a	$QAIC_c$	Δ_i	w_i
1999-2000	Pre-treatment	PC1, PC2	0.09	4	57.3	2.9	0.12
		PC1		3	54.4	0.0	0.51
		PC2		3	55.0	0.6	0.37
	Treatment	FT, PC1, PC2, FT x PC1, FT x PC2	0.83	7	43.9	6.7	0.02
		FT, PC1, FT x PC1		5	37.3	0.0	0.52
		FT, PC2, FT x PC2		5	37.5	0.3	0.46

^a Number of parameter for each model includes the intercept and the estimation from the global model of the variance inflation factor (*c*).

Table 6. Association between landscape structure (PC1-Forest integrity, PC2-Proportion of conifers), food treatment (supplementation or control) and the number of black-capped chickadees detected during playback counts. Data obtained at the center of the 24 landscapes during pre-treatment (November) and treatment (December - February) periods for the two winters of the study. Model-averaged parameters (\pm unconditional SE) were at first estimated from Poisson regressions.

	Winter 1998-1999		Winter 1999-2000	
	Pre-treatment period	Treatment period	Pre-treatment period	Treatment period
Intercept	1.85 (0.14)	1.53 (0.13)	0.88 (0.16)	2.07 (0.10)
PC1	0.31 (0.13)	0.31 (0.14)	0.06 (0.07)	0.19 (0.10)
PC2	0.03 (0.04)	-0.01 (0.02)	-0.24 (0.14)	0.02 (0.02)
Food treatment*		-0.69 (0.23)		-2.34 (0.36)
Food treatment* x PC1		-0.58 (0.23)		-0.87 (0.32)
Food treatment* x PC2		0.00 (0.02)		0.01 (0.03)

* Supplementation used as reference category for parameter estimates.

Table 7. Association between landscape structure (PC1-Forest integrity, PC2-Proportion of conifers), food treatment (supplementation or control) and species richness during playback counts. Data obtained at the center of the 24 landscapes during pre-treatment (November) and treatment (December - February) periods for the two winters of the study. Model-averaged parameters (\pm unconditional SE) were at first estimated from Poisson regressions.

	Winter 1998-1999		Winter 1999-2000	
	Pre-treatment period	Treatment period	Pre-treatment period	Treatment period
Intercept	0.44 (0.14)	0.66 (0.12)	0.07 (0.13)	0.94 (0.09)
PC1	0.29 (0.12)	0.20 (0.08)	0.10 (0.08)	0.09 (0.05)
PC2	0.02 (0.04)	0.08 (0.08)	0.02 (0.07)	0.08 (0.08)
Food treatment*		-0.72 (0.21)		-1.30 (0.19)
Food treatment* x PC1		-0.29 (0.14)		-0.23 (0.10)
Food treatment* x PC2		-0.11 (0.09)		0.04 (0.09)

* Supplementation used as reference category for parameter estimate.

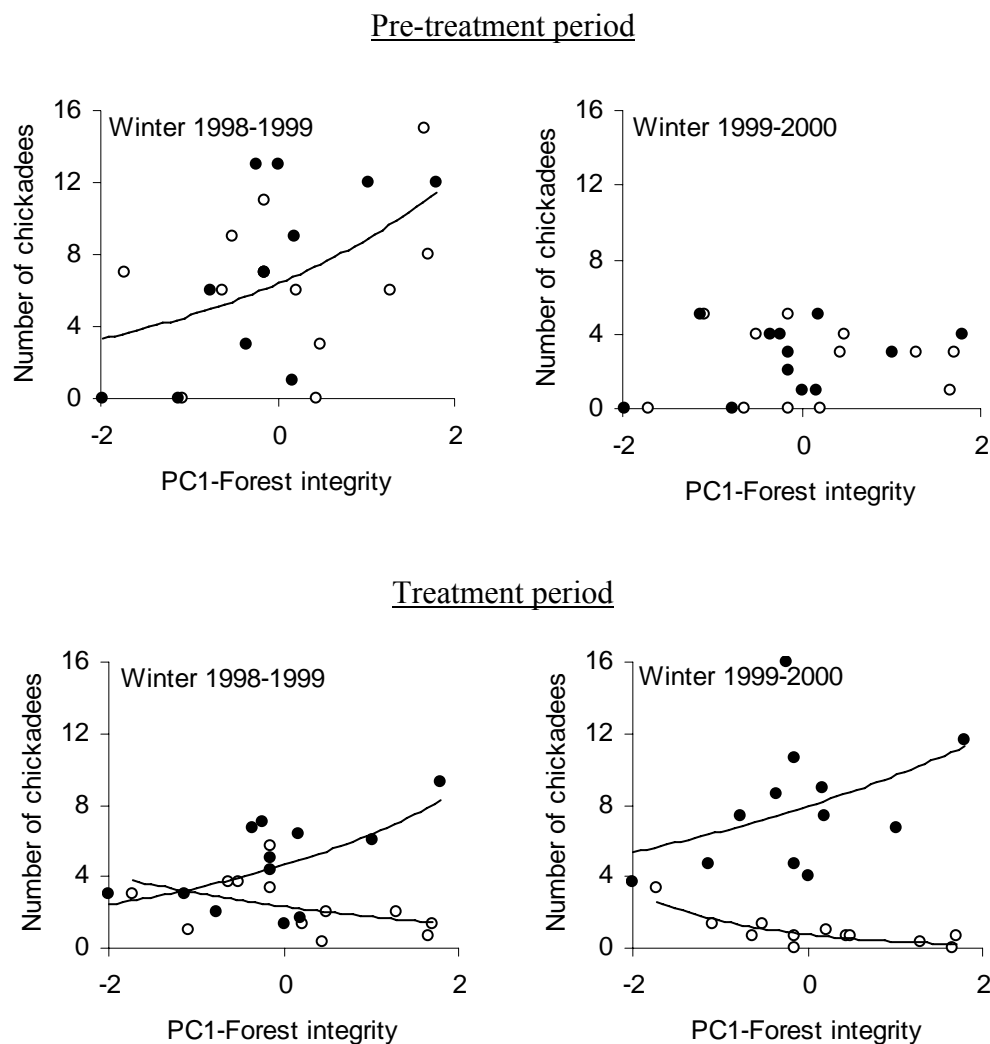


Figure 3. Relationship between forest integrity and number of black-capped chickadees detected during playback counts. Data obtained at the center of the 12 supplemented (filled circles) and the 12 control (open circles) landscapes for the two winters of the study. During pre-treatment periods (November), all landscapes were still non-supplemented. Number of chickadees during treatment periods (December - February) represents the mean of three monthly counts per landscape. The y axes were held constant to emphasize yearly variation in chickadee abundance. When zero was excluded from 95 % unconditional confidence interval of parameter estimates (effect size > 0), curves show predicted numbers of chickadees derived from Poisson regressions.

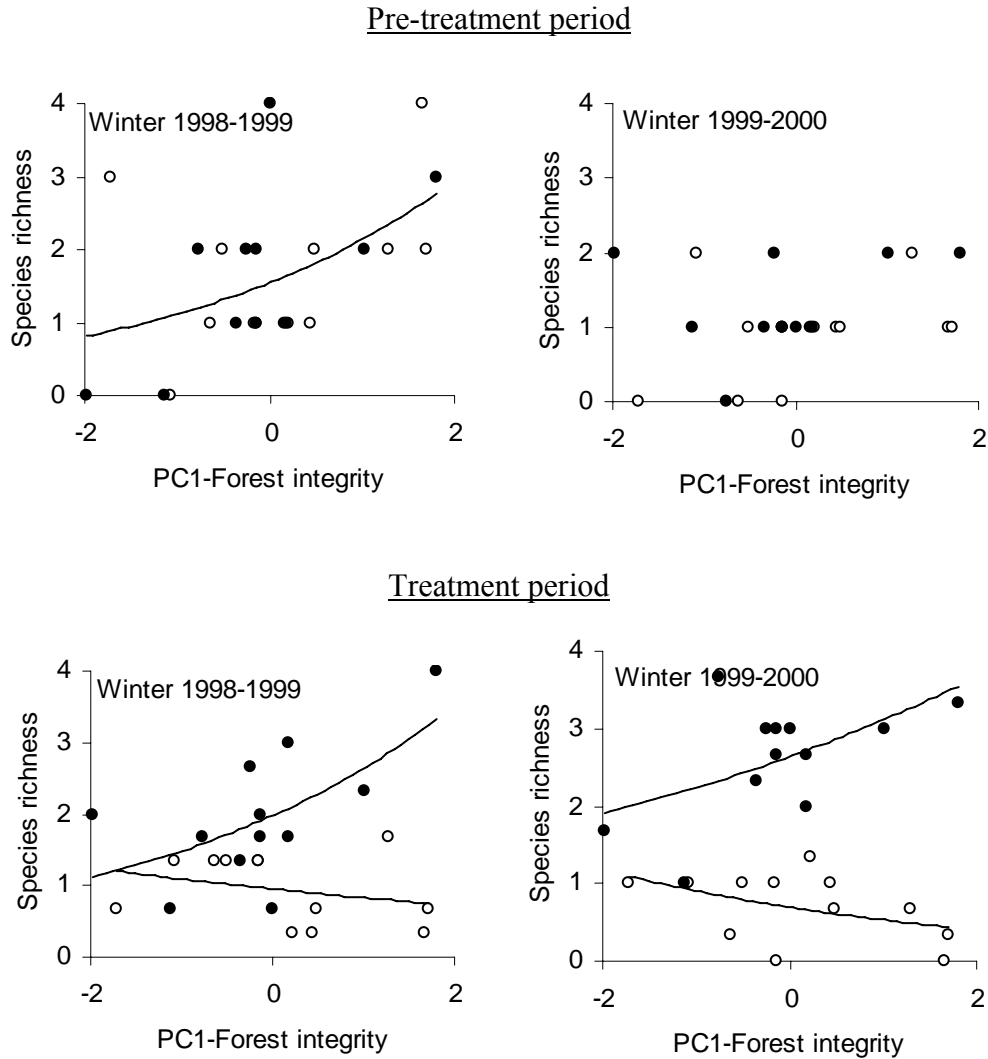


Figure 4. Relationship between forest integrity and species richness during playback counts. Data obtained at the center of the 12 supplemented (filled circles) and the 12 control (open circles) landscapes for the two winters of the study. During pre-treatment periods (November), all landscapes were still non-supplemented. Species richness during treatment periods (December - February) represents the mean of three monthly counts per landscape. The y axes were held constant to emphasize yearly variation in species richness. When zero was excluded from 95 % unconditional confidence interval of parameter estimates (effect size > 0), curves show predicted species richness derived from Poisson regressions.

Discussion

Survey results for the pre-treatment period of the first winter of the study, and in supplemented landscapes during treatment periods of both winters, all conform to most previously published studies conducted during the non-breeding season, reporting positive associations between habitat area (corresponding here to forest integrity), bird abundance (here chickadees), or species richness (e.g., Blake 1987, Telleria and Santos 1995, Doherty and Grubb 2000).

However, the positive association between PC1-Forest integrity values and black-capped chickadee numbers or species richness in supplemented landscapes during treatment periods could also be explained by landscape matrix effects, rather than only by mere habitat area effects *per se*. Resident bird populations are usually composed of adult birds with high site fidelity, already present during the breeding season, but also of dispersing first-year individuals born elsewhere (reviewed by Matthysen 1993). In the black-capped chickadee, dispersal can indeed occur throughout the winter (Weise and Meyer 1979). The presence of transient (or floater) black-capped chickadees not permanently associated to a particular home range in winter has also been documented (Smith 1984). Thus, survey results in supplemented landscapes may indicate that, in the more deforested landscapes, despite the energetic enhancement provided by food-supplementation, gaps represented movement constraints impeding the discovery and an eventual use of the center of these landscapes by black-capped chickadees, and by other species as well (as indicated by the similar effect on species richness), coming from outside the 500-m radius.

Results in control landscapes for treatment periods of both winters offer some support to the landscape matrix effects hypothesis. In contrast to pre-treatment period and supplemented landscapes treatment period results, they consistently show for each winter, decreasing, though small, trends in black-capped chickadee numbers or species richness with increasing PC1-Forest integrity values. This suggests that, in the less deforested control landscapes, birds had more opportunities to explore neighboring habitats, but furthermore, that some individuals emigrated to, more or less distant, more favorable locations. If we assume that birds are able to maximize their survival throughout the winter by some Bayesian updating process (McNamara and Houston 1980) of habitat selection

(reviewed by Block and Brennan 1993), then, many juveniles and transients could have permanently left highly forested control landscapes, when climatic conditions became harsher (during both winters of the study, there were 14 days during which the minimum temperature went below -20°C in our study area; La Pocatière climate station, *unpublished data*) and expected non-renewable food supply fell below some threshold. Similarly, Doherty and Grubb (2002) postulated that the lower apparent survival rates of first-year Carolina chickadees *P. carolinensis* they observed in forested river corridors, when compared to rates in their isolated woodlots, resulted from the on-going winter dispersal of first-year birds.

In the more deforested control landscapes, movement constraints may have left birds “gap-locked”. “Gap-locking” or the reduced ability to leave patches due to isolation has received little attention compared to constraints on the ability to reach patches. Yet, when climatic conditions deteriorate and days become shorter, exploration or emigration likely becomes too hazardous. Indeed, Grubb and Doherty (1999) found that the median distance of gaps crossed decreases from fall to late winter in the resident community they studied in Ohio. Even in the absence of the exacerbating effect of harsh climatic conditions, many studies reported that gaps and isolation represent movement constraints in forested landscapes (e.g., Bélisle et al. 2001, Cooper and Walters 2002). These constraints have also been singled out as the cause of an unusually high abundance of birds in small forest fragments (Zanette 2001).

The relatively more important disappearance of black-capped chickadees as well as the loss of species in control landscapes with high PC1-Forest integrity values could also have been interpreted as increased mortality. We consider this possibility very unlikely. Presumably, less deforested landscapes maximize the survival of birds as they offer them better protection against winds in a larger proportion of their home ranges (Dolby and Grubb 1999). Both foraging (Grubb 1977) and hoarding (Brotons et al. 2001) behaviors are indeed affected by this abiotic edge effect. Also, landscapes where forest cover is important offer access to roosting and feeding sites with few gaps to cross and therein, reduce the exposure to aerial predators such as the northern shrike *Lanius excubitor* or the northern goshawk *Accipiter gentilis*, both present in our study area. But what do we know for sure based on

previously published studies, about the relative impacts of winter mortality and emigration on forest birds? Some studies conducted in winter concluded to higher survival rates in supplemented than in control birds (e.g., Brittingham and Temple 1988), in dominants than in subordinates (Desrochers et al. 1988), and in adult than in first-year individuals (e.g., Lahti et al. 1998). As rightly acknowledged by Loery et al. (1987) and Karr et al. (1990), it is impossible, even with marked birds, to distinguish winter mortality and emigration rates in these populations, particularly for first-year dispersing birds. Survivorship rates obtained in this context, even if they take into account recapture/resighting probabilities, are nevertheless, a composite value integrating both mortality and emigration in proportions impossible to define.

To conclude, we did not demonstrate beyond any doubt that emigration occurred because, as it is the case in studies studying mortality, it is impossible to know the fate of disappearing birds in an open system like ours. However, our data suggest that differences in control landscape matrices were responsible for the variation in black-capped chickadee abundance, species richness, and patterns of spatial distribution we observed. Maybe the broad gradient of deforestation our study area allowed and the severity of local winter conditions have helped reveal this process. The counterintuitive results we obtained do not support the common assumption that mortality is the main factor behind birds' disappearance during winter. Thus, beyond the already recognized importance of large unfragmented forest patches as suitable habitats *per se* for forest birds in winter, large forest tracts appear to facilitate winter movements of at least, part of the population (e.g., subordinate juveniles). Populations of common winter residents such as black-capped chickadees may be affected only marginally by constraints to movements like those discussed above. However, those constraints may prove detrimental to populations of regionally uncommon species such as boreal chickadee and brown creeper *Certhia americana*.

Chapitre II: Landscape structure, food abundance and winter fattening strategies of black-capped chickadees

Avertissement

Le contenu de ce chapitre sera soumis d'ici la fin de 2005 à une revue de recherche en écologie animale. Hormis quelques changements mineurs dans le format ayant été nécessaires à la préparation de la thèse, le lecteur trouvera ici toute l'information contenue dans le manuscrit qui sera soumis.

Résumé

L'hiver représente un défi considérable pour les oiseaux diurnes de petite taille. L'accumulation de réserves de graisse pendant la journée doit être suffisante afin de leur permettre de survivre au jeûne nocturne et parfois même au-delà, si les conditions météorologiques au moment du lever du soleil sont défavorables. D'après les modèles théoriques, les oiseaux devraient cependant toujours chercher à minimiser leur masse, à moins que le risque de mort par inanition ne devienne trop élevé. Les stratégies journalières d'engraissement chez les oiseaux ont suscité à ce jour l'intérêt d'un grand nombre de chercheurs. Cependant, cette problématique n'a pas encore été placée dans le contexte d'oiseaux soumis à des conditions climatiques rigoureuses dans des habitats partiellement déboisés. Le but de cette étude était de vérifier si la structure du paysage et l'abondance de la nourriture avaient un effet sur la condition énergétique et les patrons quotidiens d'engraissement des oiseaux pendant l'hiver, par le biais d'une expérience d'approvisionnement en nourriture le long d'un gradient complet de déforestation. J'ai choisi la Mésange à tête noire *Poecile atricapillus* (Linnaeus), une espèce se constituant des caches de nourriture, en guise d'organisme modèle. La structure du paysage n'a eu aucun effet sur la condition énergétique des individus contrairement à l'approvisionnement en nourriture. Ce dernier résultat suggère qu'en raison du caractère stochastique des conditions météorologiques, les oiseaux bénéficiant de l'approvisionnement ont choisi d'en tirer profit, engraisant à un rythme constant tout au long de la journée, comme si le risque de mort par inanition était perçu comme étant plus immédiat que le risque de prédation. L'approvisionnement en nourriture et la progression de l'hiver ont eu un effet sur le patron quotidien d'engraissement. Dans les conditions plus clémentes du début de l'hiver, les oiseaux engraisaient à un rythme constant. Au coeur de l'hiver, les mésanges témoins, contrairement à celles bénéficiant de l'approvisionnement, engraisaient beaucoup plus rapidement pendant la deuxième moitié de la journée, minimisant ainsi les coûts associés à une masse trop élevée pendant la première moitié de la journée, sans pour autant compromettre leurs chances d'être suffisamment grasses avant la tombée de la nuit.

Abstract

At the higher latitudes, winter represents a critical energy management challenge for small diurnal birds. The daily build up of fat reserves must allow them to survive the fasting of the following night, and to withstand possible inclement weather conditions which might disrupt foraging at dawn. Theory predicts that, because of predation risks, birds should minimize their mass unless starvation risks become too high. Many modellers and empiricists have addressed winter fattening strategies in small birds. However, studies published so far have not been placed into a landscape context, despite well-documented effects of landscape structure on key aspects of the ecology of birds exposed to severe winters. Here, we investigate whether landscape structure and food abundance affect the energetic condition and the pattern of daily fattening in a population of wild birds during winter. We conducted a food-supplementation experiment repeated along a complete gradient of deforestation, using mass corrected for size and fat score data for the black-capped chickadee *Poecile atricapillus* (Linnaeus), a small food-hoarding passerine. Landscape structure did not affect chickadees' energetic condition. However, food-supplementation improved both surrogate measures of total body fat level. The latter result suggests that in response to weather unpredictability, they took advantage of supplementation, gaining fat at a constant rate, as if they perceived starvation to represent a more proximate risk than predation. Food-supplementation and winter progression affected the pattern of daily fattening. In the milder conditions of early winter, before the beginning of supplementation, chickadees gained fat at a constant rate. However, later during winter, control chickadees, contrary to supplemented chickadees, delayed most of their fattening toward the last half of the day, minimizing mass associated costs during the first half of the day, without compromising their chances of being fat enough at dusk.

Introduction

At the higher latitudes or at high elevations, winter represents a critical energy management challenge for endotherms. This challenge is particularly acute for small diurnal birds for several reasons. Flight, when compared to walking, is costly in terms of energy expenditure (Berger & Hart 1974; Pennycuick 1989). Moreover, their high surface area to volume ratio decreases heat conservation (Calder 1984; Ahlborn & Blake 2001). In temperate and boreal ecosystems, sub-zero temperatures may persist almost without interruption for months, food supply steadily decreases, day length greatly limits time available for foraging, and they must endure long fasting at night. They further have to cope with a marked unpredictability of resource access because snow and freezing rain storms periodically compromise movements, or make extensive parts of their foraging substrate inaccessible.

During winter, the daily build up of fat reserves (reviewed by Blem 1990) must allow small birds to survive the fasting of the following night, and to withstand possible inclement weather conditions which might disrupt foraging at dawn. Small birds must sometimes forage intensively to reach sufficient fattiness (7-15 % of fat-free body mass in passerines; Lehikoinen 1987). However, getting fat is costly. Foraging has been shown to decrease vigilance (Caraco 1979) and to increase exposure to predators (Lima 1986). Furthermore, the resulting mass gain increases mass-dependent energy expenditure which in turn increases foraging time necessary for maintenance of a higher level of fat (McNamara & Houston 1990 but see McNamara, Ekman & Houston 2004). Moreover, mass gain increases wing load (Pennycuick 1989), impairs flight ability to escape from predator attacks (Krams 2002), and hence presumably, above some threshold, increases predation risk (Metcalf & Ure 1995). Therefore, according to the “mass-dependent predation hypothesis”, birds should minimize their mass in order to minimize predation risk, unless starvation risks become too high (Witter & Cuthill 1993). Indeed, even during winter, birds maintain fat levels below their physiological capacity (Pravosudov & Grubb 1997a). Thus, fat levels are considered to represent a trade-off between starvation and predation risks that would maximize survival probability (Lima 1985 but see Pravosudov & Grubb 1998a). It follows that the amount of fat carried by a bird at any moment during

the day should reflect the relative importance of associated costs and benefits, as a function of time available before sunset, expected rate of gain, and current and foreseeable climatic conditions.

Over the last two decades, many researchers have addressed winter daily foraging routines, fattening, and the external energy storage strategy of food hoarding in small birds, both from theoretical (e.g. Houston & McNamara 1993; Clark & Ekman 1995; Brodin & Clark 1997; Pravosudov & Lucas 2001) and empirical (e.g. Pravosudov & Grubb 1997b; Lilliendahl 2002; Koivula, Orell & Lahti 2002; Macleod *et al.* 2005) perspectives. However, models and field studies published so far have not been placed into a landscape context, despite reported effects of landscape structure (patch size, isolation, etc.) on key aspects of the ecology of birds during the non-breeding season, particularly abundance (e.g. Blake 1987 but see Hamel, Smith & Wahl 1993), survival (Doherty & Grubb 2002 but see Matthysen 1999), emigration constraints and spatial distribution (Turcotte & Desrochers 2005), and anti-predator behaviour (Tellaria *et al.* 2001; Turcotte & Desrochers 2003).

Here, we investigate whether landscape structure and food abundance affect the fattening strategy of black-capped chickadee *Poecile atricapillus* (Linnaeus), a small (10-14 g; Smith 1991) food-hoarding passerine (e.g. Brotons, Desrochers & Turcotte 2001), exposed to severe winters. Specifically, we measure how their energetic condition and pattern of daily fattening respond to a food-supplementation experiment repeated along a complete gradient of deforestation. We test the following predictions:

1. Because fragmented forests are presumed costly from an energetic point of view (Hinsley 2000), deforestation would lower body mass index and fat score values in birds.
2. Assuming that natural food supply is limiting black-capped chickadee populations during winter (Brittingham & Temple 1988), this effect of deforestation would not be present with food supplementation.
3. Because of the severe climatic conditions prevailing in our study system (requiring birds to be relatively fat at dusk), we would observe the appearance over the winter of the

pattern of delayed daily fattening modeled by McNamara, Houston & Krebs (1990) for hoarding species having to trade-off starvation risk and mass associated costs (predation risk and higher energy expenditure).

4. Assuming that birds are able to adjust their feeding decisions and optimize their body reserves according to predictors of foraging uncertainty (e.g. Rogers & Smith 1993; Macleod *et al.* 2005), the predictability in energy gain provided by food supplementation would further delay the daily fattening, reflecting a delayed shift in the relative importance of mass associated costs and starvation risk.

Materials and methods

Study area and experimental design

This study was conducted during the winters of 1998-1999 and 1999-2000, from November through March, on the south-east shore of the St. Lawrence River estuary, in Kamouraska County (47°30' N, 69°50' W), Quebec, Canada. The study area covers approximately 600 km² of agricultural landscape where balsam fir *Abies balsamea* (Linnaeus), quaking aspen *Populus tremuloides* (Michaux), white spruce *Picea glauca* (Moench), and paper birch *Betula papyrifera* (Marshall) dominate arboreal vegetation. It is part of the temperate cold ecoclimatic region (Ecoregion Working Group 1989). At the La Pocatière climate station, located within the study area, temperatures may get as low as -30°C during winter (Environment Canada 2005).

We selected 24 circular, 500-m radius, and non-overlapping landscapes, centered on a sharp edge between a field and a forest. A 500-m radius was chosen in order to include the core of most home ranges of black-capped chickadee winter flocks (10 - 20 ha; reviewed by Smith 1991) that would occur at the center of the landscapes, while minimizing the inclusion of habitat beyond their normal flock range. We established 12 pairs of adjacent landscapes with similar forest characteristics. The centers of these paired landscapes were separated from each other by 2.5 –5 km. This distance was chosen as we considered it large enough to reduce the likelihood that some individuals would occur in both landscapes (see Smith 1991), while small enough to provide environmental conditions (microclimate, wild food abundance, predation pressure) as similar as possible within each pair of landscapes, throughout the study area. Sunflower seeds and beef suet were provided *ad libitum* at the center of one landscape of each pair (hereafter, supplemented landscapes; as opposed to control landscapes) from the last half of November through the end of March (hereafter, treatment period; as opposed to pre-treatment period, November, before the beginning of food treatments). By this spatial interspersed of food treatments (supplementation or control) throughout the study area, we intended to eliminate the risk of confounding geographic effects. Habitations were present in the study area. As we aimed to reduce the likelihood that in control landscapes,

some birds would nevertheless benefit from food supplementation, we could not randomize the assignment of food treatments within each pair. Thus, while habitations (and eventual possible food supplementation from other sources) were indeed present in supplemented landscapes, the center of each control landscape was conversely always located at least one kilometer from the nearest habitation.

Landscape characterization

To describe the structure of the 24 landscapes under study, we used Patch Analyst (Elkie et al. 1999) to obtain, from a LANDSAT-7 satellite image taken in August 1999, the three landscape metrics that we considered, referring to both natural history (Bent 1946) and landscape ecology (Andr en 1994; Fahrig 1997) literature, the most likely to affect the energetic condition and patterns of daily fattening in black-capped chickadees. We chose forest cover (%) to quantify the area of potentially suitable habitats in the landscapes. Because edges have been shown to affect space use and foraging by forest birds during winter (Dolby & Grubb 1999; Brotons *et al.* 2001), we chose edge density (m/ha of forest) as an additional index of forest fragmentation. Finally, we used the proportion of conifers in the forest (%) to provide information about the nature of forested vegetation as we considered that, in the more fragmented landscapes, coniferous vegetation could act as wind-breakers and compensate for the lack of protection against the wind, an important cause of heat loss (Thompson & Fritzell 1988).

The 24 landscapes under study provide a broad gradient of forest cover (8–88 %), proportion of conifers in the forest (3–66 %), and edge density (65–796 m/ha) (Turcotte & Desrochers 2003). In an earlier study, we performed a principal component analysis with these landscape metrics (for additional details, see Turcotte & Desrochers 2005). We obtained a first principal component describing the amount of forested habitat in our landscapes while taking into account their level of fragmentation (hereafter, PC1-Forest integrity), and a second principal component describing the relative abundance of conifers (hereafter, PC2-Proportion of conifers). In the present study, these two principal components are used as predictor variables describing the structure of our landscapes.

Trapping and measurements

Chickadees were captured with mist nets at the center of each landscape, throughout the daylight period, during pre-treatment (November) and treatment periods (January-March) of both winters. When captures started during the treatment period, food treatments were already in their second month. The presence of feeders in supplemented landscapes during the treatment period was sufficient to attract and capture birds. During the pre-treatment period, and in control landscapes during the treatment period, we used playbacks of mobbing calls of black-capped chickadees (Turcotte & Desrochers 2002) to attract birds toward the nets. Reluctance to fly toward playbacks could have induced potential sex, age or condition bias. We consider this possibility unlikely as it has been demonstrated that playbacks of mobbing calls do not affect the perception of predation risk by black-capped chickadees under cover (Desrochers, Bélisle & Bourque 2002).

The capture time for each bird was recorded to the nearest minute. All birds were banded with a U.S. Fish and Wildlife Service aluminium band to allow the identification of individuals captured on more than one occasion. During the pre-treatment period, age could be determined by the amount of wear on their outermost rectrices (Pyle 1997).

All measurements were taken by one of us (YT) thus eliminating among-observers variability which potentially, could obscure patterns of natural variability. Wing lengths (chord) were recorded to the nearest 0.5 mm with a stopped steel rule. As we often observed bent wings due to cavity roosting, only the longest wing value for each bird was considered. Tarsus length is a relatively difficult measurement to perform on live birds with calipers (Pyle 1997). Thus, tarsus lengths were also measured to the nearest 0.5 mm with a stopped steel rule. The tibiotarsus-tarsometatarsus articulation was then held against the end-stop of the rule and the length was read at the level of the last scale leg scale before the toes emerge. This unconventional method results in slightly longer readings than when tarsus length is evaluated with callipers from the depression in the angle of the intertarsal joint and the distal end of the last leg scale before the toes emerge. Though the use of a stopped steel rule does not offer as much accuracy (the closeness of a measured value to its true value; Sokal & Rohlf 1981) as the caliper method, it is much easier and faster to perform in the field on small birds, and we found values obtained in

this manner were more repeatable. Tarsus length measurements were averaged to provide a mean tarsus length for each bird thus reducing the impact of potential measurement errors. Finally, body mass was determined to the nearest 0.1 g with an electronic scale.

Evaluation of energetic condition

Energetic (or body or nutritional) condition (or state or status) was evaluated with two of the most frequently used, non-invasive techniques applicable to small birds as surrogate measures of total body fat level. We used estimation of the amount of visible subcutaneous fat deposits in the tracheal pit (or furcula or interclavicular depression) (hereafter, fat score), and mass corrected for structural size (hereafter, body mass index) as response variables. By taking these two different approaches, we wanted to strengthen the empirical evidence, or not thereof, that would provide constant results.

Fat score (or class) was evaluated immediately following capture, to avoid subjectivity that could have resulted otherwise if preceded by structural size or mass measurements. We used the classification of Gosler (1996) in which scores range from 0 (no visible fat in the tracheal pit) to a maximum of 5 (fat filling tracheal pit, bulging and overlying pectoral muscle). Fat score was found to be linearly related to claviculo-coracoid fat mass (Redfern *et al.* 2000), total body fat reserves (Blem 1990 but see Kaiser 1993) and total body mass (Kullberg, Jakobsson & Fransson 2000) in some species of passerines. However, to our knowledge, no such data exist for the black-capped chickadee.

We consider body mass index to represent a more sensitive (since not restrained to a limited number of classes) and more objective procedure (particularly when the visible amount of fat is near the limit of two adjacent classes) than the evaluation of fat score. However, the use of body mass index has been criticized because it must be assumed that a given size character varies isometrically with body size (Blem 1984). This represents an unlikely issue because, due to strong natural selection against nonfunctional relative sizes, scaling relationships between appendages and body size show low intraspecific variation around average allometries (Frankino *et al.* 2005). Nevertheless, it is noteworthy that body mass index cannot tease apart the contributions of fat and undigested gut contents to body mass.

In many published studies, body mass index is obtained by dividing mass by one size character raised to the third power (e.g. Winker, Warner & Weisbrod 1992; Yong & Moore 1993; Dunn 2001). However, such cubic transformations are not recommended (Greenwood 2003). Winker (1995) found indeed that, despite the volumetric nature of mass, cubed size character values were less accurate than unmodified values to predict actual fat content of Tennessee warblers *Vermivora peregrina*. Therefore, we used as others (e.g. Winker 1995; Merom, Yom-Tov & McClery 2000; Dunn 2002), an untransformed size character, and calculated body mass index by dividing body mass by mean tarsus length ($BMI = 10 \times \text{Mass}/\text{Tarsus}$). We preferred tarsus length to wing length as an indicator of structural size because, as in most passerines (Pyle 1997), juvenile primaries were shorter than adult primaries in this chickadee population (Fig. 1). Using wing length would have therefore systematically overestimated condition of shorter winged juveniles, all other factors (skeleton size, fat mass, body mass) being equal. Furthermore, the use of skeletal features is considered preferable because wing length also varies with physical wear (Brown 1996).

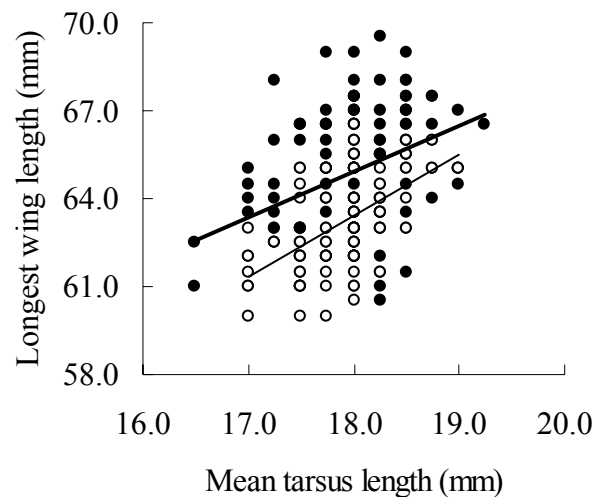


Figure 1. Relationship between mean tarsus length and longest wing length of 212 black-capped chickadees of known age. Open circles and thin line represent 79 juveniles, and filled circles and bold line represent 133 adults.

Statistical analysis

Energetic condition.-Regressions with normal or binomial error distributions were used to analyze models including the two principal components describing landscapes, food treatment, and time elapsed since sunrise at the time of capture (expressed as a percentage of total day length between sunrise and sunset; La Pocatière climate station, unpublished data) as predictor variables, and respectively, body mass index or fat score as response variables. Distinct analyses were run for pre-treatment and treatment periods but data of both winters were pooled because of otherwise insufficient sample sizes in control landscapes.

The debate persists about the proper way of analyzing fat scores (e.g. Brown 1996; Rogers 2003). We decided to consider them as ordered categorical data. We first conducted a polytomous response (fat scores 0-1 or 3 or 4 or 5) logistic regression for the treatment period but had to content ourselves with a dichotomous response (fat scores 1-2 or 3-4-5) logistic regression for the pre-treatment period because, in this case, data did not meet the proportional odds assumption (Stokes, Davis & Koch 2000). This assumption meant that, taking into account the full model of predictor variables, the likelihood of passing from one fat score category to the next had to be constant. All statistical analyses were carried out with SAS 8.1 (SAS Institute Inc. 1999).

We adopted an information-theoretic approach (see Burnham & Anderson 2002; Stephens *et al.* 2005) for the interpretation of regression results. We first assessed goodness-of-fit of global models relying on the coefficient of determination (R^2), the Hosmer and Lemeshow statistic or the Pearson statistic for, respectively, normal regressions, dichotomous response and polytomous response logistic regressions. These statistics were used as an indication of whether any of the models within a set, despite noise and randomness, could represent an acceptable approximation to an “unknown reality or truth” (Burnham & Anderson 2001). We turned afterward to the number of estimable parameters (K_i), second-order version of the Akaike’s information criterion (AIC_c), information criterion difference (Δ_i), and Akaike weight (w_i), to assess the strength of evidence supporting each of these models. Finally, in order to evaluate the

relative importance of the predictor variables considered, we referred to parameter estimates and unconditional standard errors obtained by multimodel inference. Not all possible candidate models were used in the analyses. Based on the existing literature reporting the effect of time of day on the mass of northern birds during winter (e.g., Graedel & Loveland 1995; Koivula *et al.* 2002), all models considered here included, time elapsed since sunrise at the time of capture, in combination with one or more of the other predictor variables and relevant interaction terms.

Patterns of daily fattening.-Patterns of daily fattening were addressed with tests for quadratic effect from body mass index data.

Results

For birds captured on more than one occasion during this study (57 individuals: most of them in supplemented landscapes, during the pre-treatment period and later during the treatment period), only one randomly selected observation was considered in the analysis to avoid pseudoreplication (Hurlbert 1984). This represents 161 birds for the pre-treatment period and for the treatment period, 64 and 486 birds, respectively, in control and supplemented landscapes. These 711 birds captured throughout the daylight period are considered independent sampling units of the population of all birds present in the 24 landscapes under study.

Energetic condition

Based on goodness-of-fit statistics, we considered that normal (pre-treatment period: $R^2 = 0.12$; treatment period: $R^2 = 0.20$) and logistic (pre-treatment period: Hosmer and Lemeshow, $P = 0.23$; treatment period: Pearson, $P = 0.88$) regression models did not lack fit. During the pre-treatment period, all candidate models were closely equivalent to predict body mass index (Table 1) or fat score (Table 2) as indicated by the low information criterion differences (Δ_i). Time elapsed since sunrise was the only predictor variable associated (positively) with both body mass index (Table 3) and fat score (Table 4). Before running normal regressions for the treatment period, body mass index values were log-transformed (hereafter, log body mass index) to homogenize residual variance. During the treatment period, the best models all included food treatment and time elapsed since sunrise to predict log body mass index (Table 1) or fat score (Table 2). Accordingly, food treatment and time elapsed since sunrise were the only predictor variables associated (positively) with both log body mass index (Table 3) and fat score (Table 4). For tables readability, three-way interaction terms (principal components describing landscapes structure X food treatment X time elapsed since sunrise) for which zero was included within 95% unconditional confidence interval of parameter estimates (effect size ≤ 0), and intercepts, are not shown.

Table 1. Comparison of normal regression models for the association between landscape structure (PC1-Forest integrity, PC2-Proportion of conifers), food treatment (FT; supplementation or control), time elapsed since sunrise (TS; proportion (%) of total day length) and body mass index (pre-treatment period) or log body mass index (treatment period) of black-capped chickadees. Data obtained at the center of the 24 landscapes during pre-treatment (November) and treatment (January-March) periods. Notation for the information-theoretic approach follows Burnham and Anderson (2002).

Period	Predictor variables	K_i^a	AIC_c	Δ_i	w_i
Pre-treatment	PC1, PC2, TS, PC1 x TS, PC2 x TS	7	108.9	2.0	0.19
	PC1, TS, PC1 x TS	5	108.0	1.2	0.29
	PC2, TS, PC2 x TS	5	106.9	0	0.52
Treatment	FT, PC1, PC2, TS, FT x TS, PC1 x TS, PC2 x TS, FT x PC1 x TS, FT x PC2 x TS	11	-2542.1	0.1	0.44
	FT, PC1, TS, FT x TS, PC1 x TS, FT x PC1 x TS	8	-2534.8	7.5	0.01
	FT, PC2, TS, FT x TS, PC2 x TS, FT x PC2 x TS	8	-2542.2	0	0.46
	PC1, PC2, TS, PC1 x TS, PC2 x TS	7	-2534.9	7.3	0.01
	FT, TS, FT x TS	5	-2536.5	5.8	0.03
	PC1, TS, PC1 x TS	5	-2536.7	5.6	0.03
	PC2, TS, PC2 x TS	5	-2536.1	6.2	0.02

a Number of parameter for each model includes the intercept and the residual variance.

Table 2. Comparison of logistic regression models for the association between landscape structure (PC1-Forest integrity, PC2-Proportion of conifers), food treatment (FT; supplementation or control), time elapsed since sunrise (TS; proportion (%) of total day length) and fat score of black-capped chickadees. Data obtained at the center of the 24 landscapes during pre-treatment (November) and treatment (January-March) periods. Notation for the information-theoretic approach follows Burnham and Anderson (2002).

Period	Predictor variables	K_i^a	AIC_c	Δ_i	w_i
Pre-treatment	PC1, PC2, TS, PC1 x TS, PC2 x TS	6	137.8	1.7	0.18
	PC1, TS, PC1 x TS	4	136.1	0	0.43
	PC2, TS, PC2 x TS	4	136.3	0.2	0.39
Treatment	FT, PC1, PC2, TS, FT x TS, PC1 x TS, PC2 x TS, FT x PC1 x TS, FT x PC2 x TS	10	1807.2	110.1	0
	FT, PC1, TS, FT x TS, PC1 x TS, FT x PC1 x TS	7	1799.8	102.7	0
	FT, PC2, TS, FT x TS, PC2 x TS, FT x PC2 x TS	7	1800.4	103.2	0
	PC1, PC2, TS, PC1 x TS, PC2 x TS	6	1793.1	96.0	0
	FT, TS, FT x TS	4	1697.1	0	1
	PC1, TS, PC1 x TS	4	1787.8	90.6	0
	PC2, TS, PC2 x TS	4	1787.8	90.7	0

a Number of parameter for each model includes the intercepts.

Table 3. Association between landscape structure (PC1-Forest integrity, PC2-Proportion of conifers), food treatment (FT; supplementation or control), time elapsed since sunrise (TS; proportion (%) of total day length) and body mass index (pre-treatment period) or log body mass index (treatment period) of black-capped chickadees. Data obtained at the center of the 24 landscapes during pre-treatment (November) and treatment (January-March) periods for the two winters of the study. Model-averaged parameters (\pm unconditional SE) were at first estimated from normal regressions. Parameter estimates for which zero is excluded from the 95% unconditional confidence interval (effect size > 0) appear in bold.

	Pre-treatment period	Treatment period
PC1	0.0140 (0.0286)	-0.0003 (0.0016)
PC2	0.0128 (0.0425)	-0.0076 (0.0038)
TS	0.0040 (0.0010)	0.0004 (0.0001)
PC1 x TS	0.0001 (0.0006)	0.0000 (0.0000)
PC2 x TS	-0.0008 (0.0007)	0.0000 (0.0001)
FT *		-0.0172 (0.0073)
FT * x TS		0.0003 (0.0002)

* Supplementation used as reference category for parameter estimates.

Table 4. Association between landscape structure (PC1-Forest integrity, PC2-Proportion of conifers), food treatment (FT; supplementation or control), time elapsed since sunrise (TS; proportion (%) of total day length) and fat score of black-capped chickadees. Data obtained at the center of the 24 landscapes during pre-treatment (November) and treatment (January-March) periods for the two winters of the study. Model-averaged parameters (\pm unconditional SE) were at first estimated from logistic regressions. Parameter estimates for which zero is excluded from the 95% unconditional confidence interval (effect size > 0) appear in bold.

	Pre-treatment period	Treatment period
PC1	-0.0511 (0.3506)	0.0000 (0.0000)
PC2	-0.1650 (0.3690)	0.0000 (0.0000)
TS	0.0583 (0.0109)	0.0607 (0.0052)
PC1 x TS	0.0015 (0.0078)	0.0000 (0.0000)
PC2 x TS	0.0010 (0.0068)	0.0000 (0.0000)
FT *		-0.5602 (0.2357)
FT * x TS		0.0037 (0.0048)

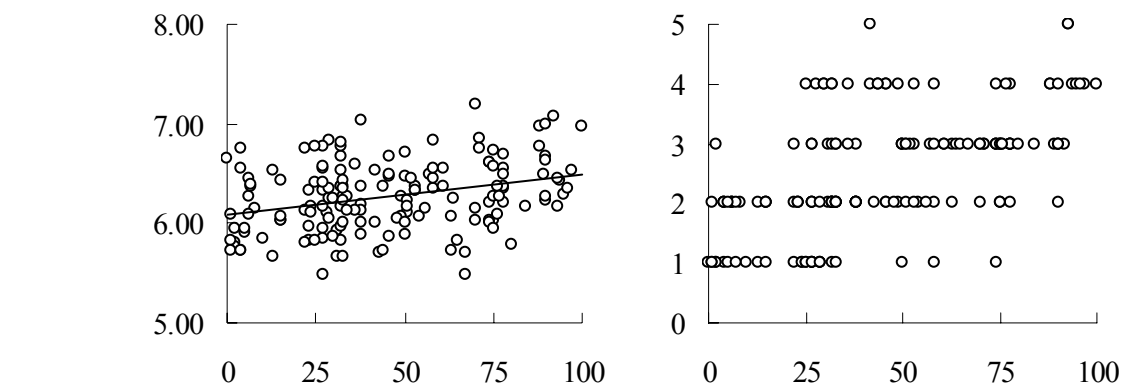
* Supplementation used as reference category for parameter estimates.

Patterns of daily fattening

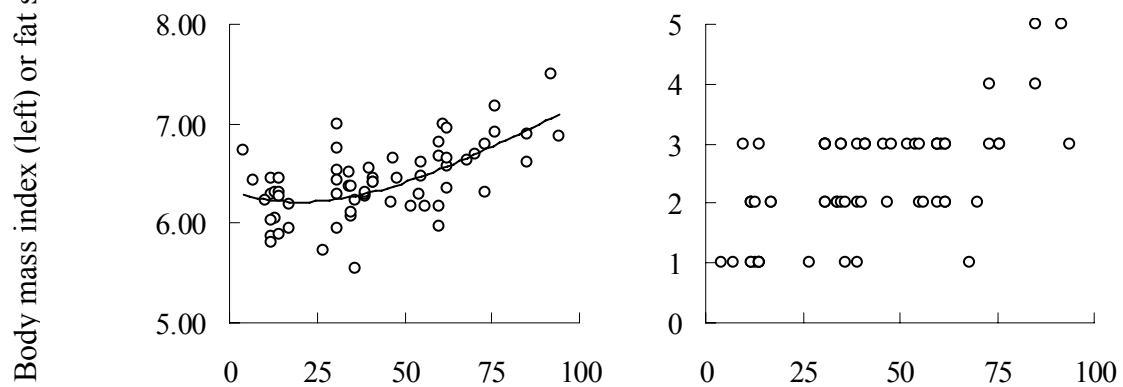
The relationship between time elapsed since sunrise and body mass index was linear during the pre-treatment period (test for quadratic effect $t_{160} = 0.71$, $P = 0.5$) and during the treatment period, in supplemented landscapes (test for quadratic effect $t_{485} = -0.06$, $P > 0.9$) (Fig. 2). However, body mass index *gain* increased with daytime in control landscapes (test for quadratic effect $t_{63} = 2.32$, $P = 0.02$) (Fig. 2).

The low sensitivity of fat score (Brown 1996) but moreover, the lack of information concerning the exact relation between fat score and total body fat reserves in the black-capped chickadee hinder the interpretation of exact patterns of daily fattening from fat score data. Nevertheless, trends in plots illustrating the relation between time elapsed since sunrise and fat score show similarities with patterns of fattening obtained from body mass index data.

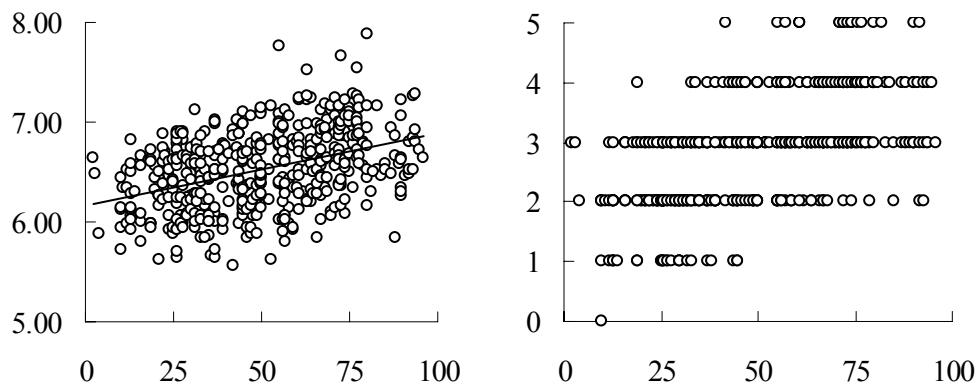
Pre-treatment period: all 24 landscapes



Treatment period: 12 control landscapes



Treatment period : 12 supplemented landscapes



Time elapsed since sunrise (% of total day length)

Figure 2. Relationship between time elapsed since sunrise (% of total day length) and body mass index ($BMI = 10 \times \text{Mass}/\text{Tarsus}$) or fat score of black-capped chickadees during pre-treatment and treatment periods for the two winters of the study. A total of 161 birds were sampled during the pre-treatment period (November), while all 24 landscapes were still non-supplemented ($R^2 = 0.10$). Respectively 64 and 486 birds were sampled in the 12 control landscapes ($R^2 = 0.39$) and in the 12 supplemented landscapes ($R^2 = 0.16$) during the treatment period (January-March). During the treatment period in control landscapes, the inclusion of a quadratic term represented an improvement of 5.5 % in the explanation of body mass index variability by time elapsed since sunrise, and a second-order polynomial curve was fitted as an indication of the relationship shape. During the pre-treatment period and during the treatment period in supplemented landscapes, the inclusion of a quadratic term did not improve the amount of variation explained by more than 0.3 %.

Discussion

The landscape context

Contrary to our first prediction, at no time during this study did we find landscape structure to have an effect on chickadees' condition. Maybe the use of independent observations of birds of different ages and sexes, captured on different days in different environmental conditions (e.g. weather) introduced too much noise to reveal any effect of landscape structure. Landscape effects, if ever present at least in some part of the population under study (e.g. subordinates), might have become apparent in a sample of marked individuals of known dominance rank, captured several times over a daytime period, simultaneously in all landscapes. Nevertheless, Telleria *et al.* (2001) also found no difference in the energetic condition of blue tits *Parus caeruleus* when they compared during winter, populations from small forest fragments and large contiguous forests in the milder climatic conditions of central Spain. Therefore, maybe energetic costs associated to partially deforested landscapes are indeed negligible. However, using ptilochronology (the measure of daily feather growth) to evaluate the effect of woodlot area on the condition of four species of woodland birds during winter in Ohio, Doherty & Grubb (2003) found a positive relation between woodlot size and feather growth in Carolina chickadees *Poecile carolinensis*, but not in the three other species they studied. Ptilochronology represents a powerful tool for assessing the energetic condition of individuals in the wild over a period of several weeks (e.g. Grubb 1989; Brodin & Ekman 1994). Contrary to daily fattening and other ineluctable body maintenance constraints, the induced growth of one or two rectrices could withstand a reduction in the energy allocated, without immediately compromising bird survival. Landscape effects, if ever present here, perhaps would have become apparent with an integrative approach spanning a much longer period of time such as ptilochronology.

The pre-treatment period

In the relatively mild conditions of the pre-treatment period (mean minimum November temperature, -3.5 °C; Environment Canada 2005), time elapsed since sunrise was the only predictor variable affecting the energetic condition of chickadees. Body mass index gain was rather linear from sunrise to sunset, in accordance with the results of Graedel &

Loveland (1995) but in contradiction with those of Lilliendahl (2002) both of whom also studied hoarding species living in mild conditions. Our results are also contradictory to model predictions for hoarding species (e.g. McNamara *et al.* 1990; Brodin 2000; Pravosudov & Lucas 2001). However, these predictions primarily concern the mid-winter period.

In November, the chickadees under study had to be moderately fat at dusk to survive the fasting of the night (Fig. 2), in accordance with the prediction of Houston & McNamara (1993) and other empiricists work (e.g. Macleod *et al.* 2005). This likely allowed them to remain all day below a wing load threshold under which their ability to escape predators was not compromised (Lind *et al.* 1999; Brodin 2000; Krams 2002), and to gain fat at a rather constant rate, scattering the risk of predation throughout the daylight period, in accordance with the “risk-spreading theorem” (Houston, McNamara & Hutchinson 1993). Predation risk was real in our study area. The northern shrike *Lanius excubitor* (Linnaeus), a major predator of black-capped chickadees during winter (reviewed by Smith 1991), was indeed regularly observed over the course of this study.

The treatment period

In the harsher conditions of the treatment period (mean minimum January-March temperature, -13.1 °C; Environment Canada 2005), only food treatment and time elapsed since sunrise had an effect (positive) on the energetic condition of birds. Using food to attract birds to capture sites could induce a condition bias as individuals in poorest condition could be most likely attracted and captured (Weatherhead & Greenwood 1981). Dufour & Weatherhead (1991) suggested that during winter, food limitation might even increase the likelihood of condition-bias. It is noteworthy that no such effect was apparent here. A positive effect of food supplementation on the energetic condition of animals living in cold environments has been reported in other studies concerning birds (e.g. Brittingham & Temple 1988; Koivula *et al.* 2002; Rogers & Heath-Coss 2003), but also mammals (e.g. Fauchald *et al.* 2004), and even fishes (e.g. Schultz & Conover 1999). However, theoretical models, assuming that birds perceive a reduced starvation risk with an increase in resource level, predict that body reserves should decrease, and hence associated costs of being fat,

when food is abundant or predictable (e.g. McNamara & Houston 1990; Houston & McNamara 1993 but see Lima 1986). Fat reserves of birds living in warm environments (low starvation risk) are indeed lower when food is abundant (see Rogers & Heath-Coss 2003).

Furthermore, not only did these birds take advantage early in the day of the overabundance and predictability of resource provided by supplementation, but contrary to our prediction, their body mass index gain was regular throughout the day. This pattern was also reported by other empiricists who studied hoarding species of high latitudes having access to supplemented food (e.g., Koivula *et al.* 2002) but again, contrasts with modellers' predictions for food hoarders (e.g. McNamara *et al.* 1990; Brodin 2000; Pravosudov & Lucas 2001). Why did birds in supplemented landscapes adopt such a strategy despite the costs of being fat? In the black-capped chickadee, the safety margin provided by fat reserves for surviving fasting in the cold is presumed to be less than a day (Chaplin 1974). Therefore, we suggest that because of the periodical unforgiving cold spells and stormy conditions (compromising access to the resource) prevailing in our study area, birds in supplemented landscapes did not perceive such a reduced starvation risk but rather, that they perceived starvation to represent a more proximate risk than predation. Their high energetic condition throughout the daylight period would thus have represented a buffer against stochastic periods of starvation due to weather unpredictability, in accordance with the "unpredictable-episode hypothesis" (Pravosudov & Grubb 1997a). Furthermore, as chickadees in supplemented landscapes likely remained close to the food source throughout the day, and thus spent less time flying than those foraging in control landscapes, their costs of being fat would have been reduced.

During the treatment period in control landscapes, chickadees delayed most of their fattening toward the last half of the day. Such a strategy would appear risky, unless their expected afternoon energy gain was predictable enough. This suggests that they then retrieved food hoarded during the first part of the day. The general pattern we observed offer support to the prediction of McNamara *et al.* (1990) for hoarding species. To our knowledge, this represents the first empirical evidence supporting this model but furthermore, reporting a seasonal change in the daily fattening pattern of a food-hoarding

species in natural conditions. Our results suggest that at this time of the year in the context of the environmental conditions (severe climate, declining food supply) prevailing in our study system, intensively foraging chickadees, by means of a reduced wing load, minimized predation risk during the first half of the day but furthermore, mass-dependent energy expenditure. As they did not benefit from an overabundance of food as in supplemented landscapes (but see Pravosudov & Grubb 1998b), chickadees, by adopting this energy-wise delayed fattening strategy, did not compromise their chances of being fat enough at dusk to survive up to around 15 hours of fasting at night in our study area.

Chapitre III: Landscape-dependent response to predation risk by forest birds

Avertissement

Le contenu de ce chapitre a été publié en mars 2003. Hormis quelques changements mineurs dans le format ayant été nécessaires à la préparation de la thèse, le lecteur trouvera ici toute l'information contenue dans :

Turcotte, Y, and A. Desrochers. 2003. Landscape-dependent response to predation risk by forest birds. *Oikos* 100: 614-618.

Résumé

Notre compréhension en profondeur des effets de la déforestation et de la fragmentation de la forêt sur les effectifs des populations d'oiseaux nécessite la connaissance des mécanismes sous-jacents. J'ai conçu une expérience dont le but était de déterminer si la déforestation avait un effet sur le comportement anti-prédateur de Mésanges à tête noire (*Poecile atricapilla*) en quête de nourriture. L'expérience a été effectuée à une bordure forêt-champ, au centre de 24 paysages représentant globalement un gradient complet de déforestation (8 – 88 % de couvert forestier, rayon de 500 m). J'ai mesuré la distance maximale jusqu'à laquelle les bandes de mésanges s'aventuraient à l'intérieur du champ pour aller chercher des graines de tournesol. J'ai utilisé cette valeur en guise d'indicateur de leur propension à s'exposer au risque d'être victime d'un prédateur. Dans les paysages témoins, les mésanges se sont aventurées plus loin à l'intérieur du champ lorsque le déboisement était marqué, parfois même jusqu'à la distance maximale de 40 m imposée par le dispositif expérimental. Dans les paysages expérimentaux, les mésanges avaient bénéficié d'un approvisionnement en nourriture de plusieurs semaines avant la tenue de l'expérience. Celles-ci, contrairement aux mésanges des paysages témoins, demeuraient toujours près de la bordure, choisissant ainsi la protection conférée par le couvert forestier. Ces résultats suggèrent que la déforestation augmente vraisemblablement les besoins énergétiques des individus, ce qui aurait pour effet d'augmenter leur propension à s'exposer à d'éventuels prédateurs.

Abstract

Knowing how forest loss and associated fragmentation actually impact individual birds is essential to our understanding of consequences at the population level. We conducted a landscape-level experiment to test whether deforestation affects the trade-off between foraging and antipredatory behaviour of Black-capped Chickadees (*Poecile atricapilla*) in 24 landscapes (range 8 – 88 % forest cover, 500-m radius) during two winters. At a field-forest edge in the centre of each landscape, we used the maximum distance ventured into the open by flocks to get sunflower seeds placed on the snow-covered fields, as a measure of risk-taking. In the more deforested landscapes, chickadees ventured farther (up to the maximum of 40 m) into the open. Edge density and proportion of conifers in the forest had no influence on risk-taking. However, where *ad libitum* food was available for a few weeks prior to the experiment (in 12 of the 24 landscapes), chickadees ventured four meters or less away from the forest edge, regardless of the level of deforestation. We conclude that landscape deforestation increases energy stress, which in turn promotes risk-taking, and may therefore increase winter mortality through greater exposure to predators.

Introduction

Forest loss and associated fragmentation are probably the most publicised causes of the decline of temperate, terrestrial bird populations (Terborgh 1989), despite the controversial nature of current evidence (Haila et al. 1993, Harrison and Bruna 1999). Contributing to the controversy is a limited understanding of how changes in landscapes actually impact individuals. During the breeding season, deforestation and associated landscape changes can reduce food supply (Burke and Nol 1998, Zarette et al. 2000), lead to lower nesting success (Robinson et al. 1995, Crooks and Soulé 1999) and limit nesting opportunities through edge avoidance during nest-site selection (Huntau et al. 1999). Deforestation may further reduce mobility (Bélisle et al. 2001, Rodriguez et al. 2001) and therefore, could compromise dispersal, recruitment and pairing success (Gibbs and Faaborg 1990, Villard et al. 1993) in relatively isolated forest patches. Other possible consequences of deforestation on bird populations have received comparatively little attention, especially outside the breeding season.

During winter at northern latitudes, forest birds must forage all day in order to survive sub-zero temperatures. For several months, they have to cope with a decreasing food supply, short daylight period and long fasting at night. When foraging, small endothermic birds appear to trade-off energy gains with safety against predators (Lima and Dill 1990, Lima and Bednekoff 1999). Food limitation (Boutin 1990, Doherty and Grubb 2002) and predation (Jansson et al. 1981) are indeed the main factors causing mortality among them in winter. In deforested landscapes, increased energetic cost of movements through gaps (Hinsley 2000) or an unfavourable thermal environment (Dolby and Grubb 1999) will add to energetic stress and can result in a lower survivorship (Doherty and Grubb 2002). Such an ecological context is expected to promote foraging efficiency at the expense of antipredatory behaviour (Houston and McNamara 1993).

We conducted a behavioural experiment to test whether landscape-level deforestation affects the trade-off between feeding and safety from predators in small forest birds during winter, using the Black-capped Chickadee (*Poecile atricapilla*), as a model species. This small (~11 g) permanent-resident species inhabits forests throughout the northern part of

North America, where it forms winter flocks of 2-12 individuals (Smith 1991). Flocking likely favours its survival as it presumably increases foraging efficiency and reduces predation risk (Pulliam 1973, Matthysen 1990). Two other adaptations, food hoarding (Shettleworth et al. 1995, Brotons et al. 2001) and hypothermia (Chaplin 1974, 1976) on cold nights are assumed to help this species maintain its energetic balance and therein, likely contribute to maximise its fitness.

Methods

This study was conducted in January-February 2000 and 2001 on the south shore of the St. Lawrence River estuary, in Kamouraska County, Quebec, Canada (47°30' N, 69°50' W). The study area covered approximately 600 km² of agricultural landscape. Balsam Fir (*Abies balsamea*), Quaking Aspen (*Populus tremuloides*), White Spruce (*Picea glauca*) and Paper Birch (*Betula papyrifera*) dominate forest vegetation. The study area is part of the Temperate Cold ecoclimatic region (Ecoregion Working Group 1989). At the La Pocatière climate station, located within the study area, daily mean temperatures (1971-2000) for January and February, the coldest winter months, are respectively -11.7 °C and -10.3 °C (Environment Canada 2002). At this latitude, day length at winter solstice is 8 h 28 min.

In the context of a larger study of Black-capped Chickadee winter ecology, we selected 24 circular, 500-m radius, and non-overlapping landscapes, centred on a sharp edge between a field and a forest. We chose this radius in order to include the core of most home ranges (10-20 ha; reviewed by Smith 1991) of Black-capped Chickadee winter flocks occurring at the centre of the landscapes. Based on a LANDSAT-7 satellite image taken in August 1999 and analysed with Patch Analyst (Elkie et al. 1999), these landscapes provided a broad gradient of forest cover, edge density and proportion of conifers in the forest (Table 1, Fig. 1).

Table 1. Description of the 12 food-supplemented and the 12 control landscapes used in behavioural trials.

Landscape metric	Food-supplemented landscapes			Control landscapes		
	Minimum	Mean	Maximum	Minimum	Mean	Maximum
Forest cover (%)	8	45	88	10	53	87
Edge density (m/ha)	65	261	796	70	241	597
Conifers (%)	12	26	39	3	21	66

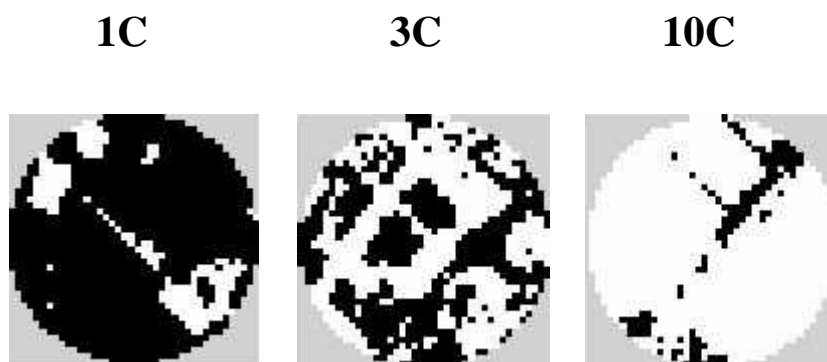


Figure 1. Three control landscapes (500-m radius) used in behavioural trials. Forests are in black, open habitats (mostly agricultural fields) in white. Each pixel corresponds to a 25 m X 25 m surface. 1C: forest cover = 86 %, edge density = 73 m/ha. 3C: forest cover = 48 %, edge density = 379 m/ha. 10C: forest cover = 10 %, edge density = 597 m/ha.

We established 12 pairs of adjacent landscapes with similar forest characteristics. Prior to running the experiment, we provided sunflower seeds *ad libitum* at the field-forest edge at the centre of one landscape of each pair for at least two weeks (hereafter, food-supplemented landscapes). Chickadees respond quickly to supplemental feeding and their local abundance becomes much higher than otherwise in such circumstances (Wilson 2001). The centre of the other landscape of each pair was located at least one kilometre from the nearest habitation in order to reduce the likelihood of food supplementation from another source (hereafter, control landscapes). Food treatments (food supplementation or control) were conducted each winter.

Following the food supplementation period, we laid boards of wood (7 X 20 cm) every two meters from the forest edge to 40 m into the snow-covered field at the centre of each 24 landscapes. On each board, we placed two sunflower seeds. The black seeds against the pale board and the board itself against the snow offered strong visual contrast. In food-supplemented landscapes, we removed the feeders just before behavioural trials were made and covered with snow the seeds that fell on the ground. Chickadees were attracted to the vicinity of the edge by remotely controlled playbacks of their mobbing calls (Turcotte and Desrochers 2002). Playbacks ended and trials began when birds came within two meters of the board nearest to the forest edge.

We assumed that vulnerability to predation increases with distance from the forest edge and that birds were able to estimate predation risk. Therefore, we used the maximum distance ventured into the open to pick up seeds by any flock member as a measure of risk-taking (Caraco et al. 1980). Birds flying into the open without landing were not taken into account; we considered that they did not expose themselves to predation as much as those that landed on the boards (Hilton et al. 1999). Open habitats were assumed risky based on observations, outside of trials, of two diurnal predators, most often the Northern Shrike (*Lanius excubitor*) and once, the Northern Goshawk (*Accipiter gentilis*), in 33 % of both food-supplemented and control landscapes. Predator sightings occurred in landscapes where forest cover ranged from 8 to 87 % and were equally distributed between landscapes where forest cover was above 50 % and those where it was below 50 %. The Northern Shrike, which was observed in seven out of the 24 landscapes, could be considered as a major predator of Black-capped Chickadees during winter (reviewed by Smith 1991). Indeed, we found on a few occasions evidence of successful attacks by this predator within and nearby the study area. Typically, birds depleted seeds progressively toward the open. Trials ended when no bird landed on boards for 15 min. Consequently, the duration of trials depended on flocks' willingness to venture into the open: trials in which birds ventured farther away into the open lasted longer than those in which birds took only the seeds closest to the forest edge. We never conducted trials during the 2 hours following sunrise or preceding sunset. Thus, we avoided a potentially confounding effect that could have arisen otherwise if birds would have adopted a bimodal foraging routine, with feeding peaks near dawn and dusk (McNamara et al. 1994). Trials were conducted once per landscape to avoid behavioural habituation and to preserve the independence of the observations. Trials took place on days without strong wind or precipitation.

We used generalised linear models (type III contrasts) to analyse the effects of landscape metrics and food treatment on distance ventured into the open. The effects of potentially confounding variables (flock size, air temperature, time of day; Caraco 1979, Grubb and Greenwald 1982, McNamara et al. 1994) were addressed with Spearman rank correlations. Our small sample sizes did not allow the incorporation of these variables and their interactions with food treatment in more complex models. All statistical analyses were made with SAS (SAS Institute Inc. 1999).

Results

Neither the proportion of conifers in the forest nor edge density had an influence on distance ventured into the open by chickadees. Thus, we eliminated those variables from a preliminary model (Table 2). In preliminary and reduced (final) models, forest cover and food treatment both affected distance ventured into the open but forest cover had different effects in control and food-supplemented landscapes, as indicated by the interaction between forest cover and food treatment (Table 2, Fig. 2). In fact, birds in the food-supplemented landscapes invariably remained close (four meters or less) to the forest edge, even though they were generally present in large numbers (at least 10 or more individuals). Only birds in control landscapes ventured farther as forest cover decreased, some of them even reaching the maximal distance allowed by our experimental design (40 m away from the forest edge), where forest cover represented less than 50% of the landscape. The strong effect of forest cover in control landscapes could not be explained by flock size (range = 1 to 8 birds, $r_s = -0.11$, $P = 0.7$), air temperature (range = -17 to 0°C , $r_s = 0.00$, $P = 1.0$), or time of day (range = 9:15 to 14:00 EST, $r_s = 0.29$, $P = 0.4$).

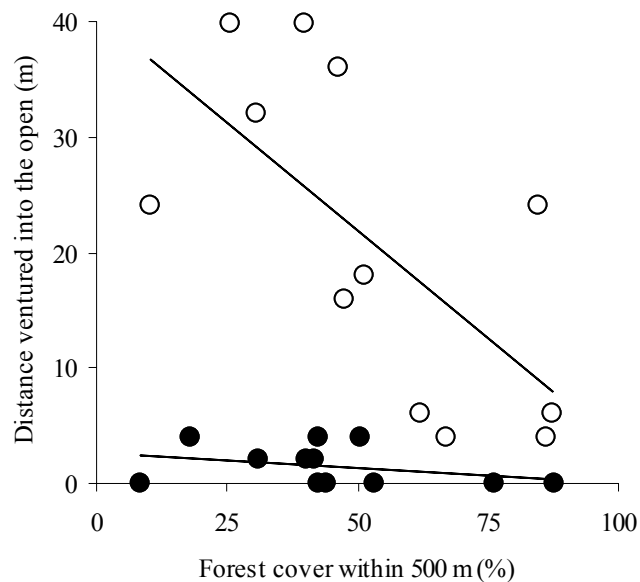


Figure 2. Relation between forest cover and maximum distance ventured into the open by foraging Black-capped Chickadees in control (open circles) and food-supplemented (filled circles) landscapes.

Table 2. Influence of food treatment and landscape structure on the maximum distance ventured into the open by foraging Black-capped Chickadees in winter. Parameters estimated from generalised linear models with type III contrasts ($n = 24$).

Parameter	Df	Preliminary model				Final model			
		Estimate	(SE)	F	P	Estimate	(SE)	F	P
Food treatment ¹	1	36.96	(7.74)	22.78	<0.001	37.94	(7.66)	24.56	<0.0001
Forest cover (%)	1	-0.17	(0.16)	6.33	0.02	-0.03	(0.11)	7.67	0.01
Food treatment ¹ X Forest cover	1	-0.32	(0.15)	4.71	0.04	-0.35	(0.14)	5.82	0.03
Edge density (m/ha)	1	-0.02	(0.02)	1.43	0.25				
Conifers (%)	1	-0.06	(0.11)	0.26	0.61				

¹ Food-supplementation used as reference category for parameter estimates.

Discussion

Irrespective of forest cover, chickadees in food-supplemented landscapes remained close to the forest and thus avoided predation risk at the expense of an immediate energy gain. As they likely enjoyed higher energy reserves (in the form of fat or hoarded food) or because they became conditioned to a less stochastic food supply, they could adopt a ‘safety-first’ strategy (Walther and Gosler 2001). By contrast, those in control landscapes ventured farther into the open as forest cover decreased. This suggests that these birds faced increased energy stress in deforested landscapes, thus leading them to forage in riskier locations.

Though we did not evaluate variability of responses among flock members, other studies suggest that socially subordinate individuals would be those who ventured first into the open (De Laet 1985) or went farther from the forest edge (Schneider 1984) and thus, were more exposed to predation. The population-level response to deforestation by wintering chickadees may thus depend on whether subordinates would have breeding opportunities if they survived (Desrochers et al. 1988). Nevertheless, considering flock members jointly, safety against potential predators was compromised for greater foraging efficiency in the more deforested landscapes. We suggest that this shift in the food versus safety trade-off will amplify winter mortality of species living in cold environments.

Conclusion générale

Cette étude a pu démontrer que la structure du paysage a des effets mesurables sur certains aspects de l'écologie des oiseaux forestiers pendant l'hiver (répartition spatiale et comportement anti-prédateur). Les résultats obtenus suggèrent de plus que les besoins énergétiques élevés des oiseaux en cette saison sont en partie responsables des effets observés puisque ceux-ci ont invariablement été différents lorsqu'une source supplémentaire de nourriture était disponible.

Dans le premier chapitre de la thèse, les résultats présentés concernant la répartition spatiale des oiseaux forestiers à la fin de l'automne sont en accord avec la vaste majorité des études ayant rapportée une association positive entre la quantité d'habitat boisé et l'abondance des individus et la richesse spécifique. Cependant pour la période correspondant au cœur de l'hiver, la relation inverse observée dans les paysages témoins suggère fortement que l'émigration des oiseaux a été facilitée dans les paysages les plus perméables, soit ceux dont la couverture forestière était la plus élevée et la moins morcelée. Les résultats divergents observés pendant le cœur de l'hiver dans les paysages expérimentaux, soit ceux ayant bénéficié d'un apport supplémentaire en énergie alimentaire, suggèrent de plus que le gain énergétique net pouvant être réalisé au cours de la quête alimentaire dans les paysages témoins était vraisemblablement insuffisant et donc, à l'origine de la désertion partielle des paysages témoins les plus boisés.

La condition énergétique et les patrons journaliers d'engraissement des Mésanges à tête noire à la fin de l'automne et au cours de l'hiver ont fait l'objet du deuxième chapitre. Il convient tout d'abord de mentionner que la structure du paysage n'a, en aucun cas, eu d'effets mesurables sur la condition énergétique des mésanges, c'est-à-dire ni à la fin de l'automne, ni au cours de l'hiver, que ce soit dans les paysages témoins ou dans les paysages expérimentaux. Hormis le temps écoulé depuis le lever du soleil, seul l'apport supplémentaire de nourriture a eu un effet mesurable sur la condition énergétique des individus. Cet effet positif suggère que les oiseaux ont tiré profit de cette source de nourriture et ce tout au long de la journée, probablement parce qu'en raison du caractère stochastique des conditions météorologiques, le risque perçu de mort par inanition

demeurait plus immédiat que le risque d'être victime de prédateurs, tel que le suggère le postulat du « *unpredictable-episode hypothesis* » (Pravosudov et Grubb 1997a). Ce résultat supporte de plus l'hypothèse évoquée au paragraphe précédent selon laquelle, la nourriture était en quantité insuffisante dans les paysages témoins et pouvait constituer un facteur limitant les populations. Il est également possible que les déplacements rendus moins importants pour les mésanges présentes dans les sites expérimentaux aient pu favoriser l'adoption d'une telle stratégie d'engraissement, les coûts associés à une augmentation de la masse (coût métabolique et risque de prédation accrus) se trouvant alors réduits.

Dans le contexte des conditions encore relativement clémentes de la fin de l'automne, avant le début de l'approvisionnement en nourriture dans les paysages expérimentaux, le patron journalier d'engraissement plutôt linéaire observé suggère que les mésanges ont alors réparti tout au long de la journée les coûts associés à une masse plus élevée, en accord avec le postulat du « *risk-spreading theorem* » de Houston et al. (1993). Plus tard dans l'hiver, les mésanges des paysages témoins se devaient d'accumuler quotidiennement une plus grande quantité de réserves graisseuses avant la nuit et ce, dans un contexte de rareté croissante de la nourriture. Celle-ci ont alors accumulé ces réserves endogènes selon un patron différent, la majeure partie de celles-ci étant rapidement accumulée pendant la deuxième moitié de la journée, probablement en partie par la récupération des réserves exogènes. Un patron semblable pour les espèces se constituant des caches de nourriture avait été prédit par McNamara et al. (1990). Les résultats présentés ici représenteraient, à ma connaissance, la première évidence empirique supportant ce modèle.

Le troisième chapitre présente les résultats d'une expérience qui s'est déroulée au cœur de l'hiver et au cours de laquelle les Mésanges à tête noire ont été confrontées au choix d'aller chercher de la nourriture jusqu'à 40 m à l'intérieur d'une ouverture, au détriment de la sécurité conférée par le couvert forestier. Étant donné que les oiseaux devaient obligatoirement s'immobiliser pour prendre possession de la nourriture, plus un oiseau faisait le choix de s'aventurer loin de la lisière boisée, plus grande était la probabilité qu'il soit capturé en cas d'attaque de la part d'un prédateur aérien déjà sur sa lancée. Les oiseaux des paysages expérimentaux étaient temporairement privés de la nourriture fournie lors de la réalisation de cette expérience. Néanmoins, ceux-ci sont toujours demeurés à proximité

de la forêt, vraisemblablement parce que leurs réserves énergétiques, tant corporelles que sous la forme de caches, ne les incitaient pas à s'exposer au risque d'être victime d'un prédateur, le risque perçu de mourir d'inanition étant alors trop faible. Par contre dans les paysages témoins, les mésanges des paysages les plus sévèrement déboisés se sont aventurées plus loin de la forêt que celles des paysages où la surface boisée était plus importante, comme si elles percevaient que le risque de mourir par inanition était plus élevé que celui d'être victime de prédation. Si les individus des milieux plus fragmentés sont davantage enclins à s'exposer ainsi aux attaques des prédateurs, on peut supposer qu'une mortalité plus élevée en découle (Hinsley et al. 1995).

Quelle vision d'ensemble peut-on avoir au terme de cette étude? De quelle manière les résultats et interprétations présentés dans cette thèse s'articulent-ils les uns aux autres? Les résultats des deux premiers chapitres nous suggèrent tout d'abord que, du point de vue des oiseaux, les conditions environnementales caractérisant la fin de l'automne sont suffisamment différentes de celles du cœur de l'hiver pour que, à moins d'un apport énergétique supplémentaire sous la forme de nourriture, les patrons de répartition spatiale et de l'engraissement journalier soient tout à fait différents entre ces deux périodes. Ces résultats démontrent à quel point les décisions comportementales (émigration et stratégie d'engraissement) des oiseaux forestiers pendant l'hiver sont largement tributaires du rendement énergétique qu'ils peuvent obtenir lors de la quête alimentaire dans un habitat. Les résultats de l'expérience présentée au troisième chapitre soulignent eux aussi l'importance de la qualité de l'habitat d'un point de vue énergétique. Cependant, comment interpréter le fait que, dans les paysages témoins, les mésanges des milieux où la déforestation était la plus marquée et ayant pris davantage de risques n'étaient pas, à la lumière des résultats présentés au chapitre II, en moins bonne condition énergétique? La condition énergétique des mésanges a été évaluée dans cette étude à l'aide de deux méthodes permettant d'estimer leurs réserves lipidiques totales à un moment précis de la journée. Les résultats auraient-ils été différents si la condition énergétique des oiseaux avait été évaluée d'une manière moins ponctuelle soit en utilisant une approche intégrative de la condition des oiseaux sur plusieurs semaines comme le permet la méthode ptilochronologique (Grubb 1989, Brodin et Ekman 1994)? Il s'agirait certainement là d'une avenue qu'il serait pertinent de considérer avant de conclure définitivement, surtout à la

lumière des résultats du troisième chapitre, que la structure du paysage n'a pas d'effets sur la condition énergétique des oiseaux pendant l'hiver.

Applications écologiques

Quelles sont les nouvelles connaissances issues de cette thèse pouvant contribuer aux efforts de gestion des habitats forestiers et de conservation des populations d'oiseaux qui les utilisent?

Les résultats présentés au premier chapitre suggèrent que les mouvements des populations sont importants pendant l'hiver mais aussi, que les habitats forestiers fragmentés nuisent alors à ces mouvements. Dès lors, un déboisement trop sévère pourrait avoir des conséquences néfastes pour les populations dont les effectifs sont au départ limités, à moins que ne soient préservés de longs corridors boisés ininterrompus, semblables à ceux qui sont laissés en place le long des cours d'eau par l'industrie forestière dans les forêts publiques. L'importance des bandes riveraines pour les mouvements de populations pendant l'été a déjà été démontrée (Machtans et al. 1996) et leur importance présumée pour les mouvements hivernaux a également été récemment évoquée par une équipe de chercheurs de l'Ohio (Doherty et Grubb 2002). Étant donnée la richesse du réseau hydrographique québécois, le potentiel des bandes riveraines à cet égard est particulièrement élevé, d'autant plus qu'elles ne peuvent en aucun cas faire l'objet d'une coupe totale dans la forêt publique. Cette dernière caractéristique leur confère un avantage indéniable sur le plan de la conservation par rapport aux lisières boisées laissées en place entre les aires de coupe dans la forêt publique. Ces dernières peuvent en effet être coupées dès que la régénération des aires de coupe adjacentes atteint une hauteur de trois mètres, tel que le permet l'article 75 de la loi sur les forêts du gouvernement du Québec (Ressources naturelles et Faune 2005). Il va sans dire que cette hauteur de trois mètres ne tient pas compte de la quantité de neige pouvant couvrir le sol pendant l'hiver. Plus grandes seront ces accumulations, moins la hauteur effective et donc la valeur réelle de ces peuplements en régénération, en tant qu'habitats ou corridors pour l'avifaune, sera importante.

Cependant, les bandes riveraines se devraient d'être d'une largeur suffisamment importante afin que ne soient pas compromises, par temps froid et venteux, la quête alimentaire (Grubb

1977) et donc ultimement, la survie des oiseaux qui les emprunteraient. À la lumière des résultats d'études récentes (Dolby et Grubb 1999, Brotons et al. 1999), cette distance serait vraisemblablement beaucoup plus grande que la largeur minimale de 20 mètres prévue selon les dispositions de l'article 2 de la loi sur les forêts (Ressources naturelles et Faune 2005). Les effets protecteurs conférés par les bandes riveraines longeant les deux rives des rivières les plus étroites peuvent certainement s'additionner, pour atténuer davantage les effets du vent. Cependant, les oiseaux présents dans les bandes riveraines des lacs et des rivières larges de plusieurs dizaines de mètres ne pourraient bénéficier de cet avantage. Si en raison d'impératifs d'ordre économique, la largeur des bandes riveraines protégée par la loi ne pouvait être augmentée de manière importante, des élargissements ponctuels mais substantiels représenteraient, à tout le moins, une amélioration par rapport à la situation actuelle.

Du troisième chapitre se dégage le constat qu'une détérioration de l'habitat peut modifier le comportement anti-prédateur des individus. Dans les habitats forestiers fragmentés où des oiseaux se rendront plus vulnérables aux attaques des prédateurs (Hinsley et al. 1995), que ce soit en traversant les ouvertures ou en exploitant les ressources alimentaires des milieux ouverts, les impacts négatifs sur les populations seront encore une fois potentiellement plus marqués chez les espèces peu abondantes. La préservation par l'industrie forestière de grandes surfaces boisées intactes s'avère dès lors essentielle à la conservation des espèces résidentes les plus sensibles à la récolte forestière, telles que dans la forêt boréale, le Pic tridactyle (*Picoides tridactylus*), le Pic à dos noir (*Picoides arcticus*) ou le Grimpereau brun (*Certhia americana*) (Imbeau et al. 1999). Ces aires protégées se devraient alors de correspondre au moins à la surface estimée des domaines vitaux hivernaux de ces espèces plus vulnérables. Malheureusement, cette information de première importance ne nous est pas toujours connue (Imbeau et Desrochers 2002).

Perspectives de recherche

Les résultats présentés dans la présente thèse ne représentent qu'une contribution somme toute modeste à notre compréhension de l'écologie hivernale des oiseaux forestiers confrontés au phénomène de la déforestation. Pour le bénéfice des étudiants gradués ou

chercheurs établis qui prendront le relais afin d'améliorer encore davantage notre compréhension de cette problématique, voici quelques suggestions de questions découlant des thèmes abordés dans la thèse. Elles se prêtent toutes à la formulation d'hypothèses falsifiables, certaines logiquement réalistes pour un étudiant ne disposant que de une à trois années tout au plus pour réaliser ses travaux d'échantillonnage, d'autres non. Notez que la plupart de ces questions font référence à des oiseaux à l'état sauvage et qui ne seraient pas nourris artificiellement.

Chapitre I

- 1) Quels sont les facteurs proximaux (p.ex. réchauffement momentané des températures après une vague de froid, diminution de la quantité de la nourriture animale en deçà d'un certain seuil, abondance des juvéniles dans la population) qui déclenchent au cours de l'hiver, l'émigration d'une partie des populations résidentes?
- 2) Qui sont surtout ces émigrants? Les juvéniles? Les oiseaux subordonnés?
- 3) De tels mouvements existe-t-il également chez une espèce telle que la Mésange à tête brune (*Poecile hudsonica*), étroitement associée aux peuplements fortement dominés par les résineux?
- 4) Dans la mesure où ces mouvements de populations seraient davantage orientés vers le sud, telle que le suggère la littérature anecdotique sur le sujet, se pourrait-il que les résultats obtenus ici ne soient qu'un artéfact découlant de la présence de l'estuaire?
- 5) De plus, obtiendrait-on les mêmes résultats dans un contexte expérimental où, sur plusieurs dizaines de kilomètres au-delà du rayon de 500 m retenu, le couvert forestier serait parfaitement, autant que faire se peut, contrôlé?

Chapitre II

- 1) Il serait peut-être possible d'analyser les effets de la structure du paysage en considérant la condition énergétique des mêmes individus, idéalement de statut hiérarchique connu,

capturés à quelques reprises au cours d'une même journée. Une telle approche, dite longitudinale, nous conduirait-elle aux mêmes conclusions?

2) L'évaluation des effets de la structure du paysage sur la condition des Mésanges à tête noire par une approche ptilochronologique (Grubb 1989, Brodin et Ekman 1994) nous conduirait-elle aux mêmes conclusions?

3) Les relations de dominance à l'intérieur des bandes auraient-elles un effet sur la croissance des plumes ainsi induite?

4) La relation entre le *fat score* et les réserves lipidiques ou la masse des individus d'une même taille (ce qui éviterait de sacrifier des individus) est-elle linéaire comme cela semble être le cas chez d'autres espèces (Blem 1990, Kullberg et al. 2000)

5) De quelle manière varient précisément, mois par mois, la condition énergétique et le patron d'engraissement des Mésanges à tête noire?

6) De quelle manière varient non seulement mois par mois, mais aussi à différentes latitudes, la condition énergétique et le patron d'engraissement des individus des espèces résidentes les plus communes?

7) Les enregistrements des cris de houspillage de la Mésange à tête noire attirent-ils avec la même efficacité les individus d'âge, de sexe et de condition énergétique différentes?

Chapitre III

1) Qui sont les individus qui, à l'intérieur des bandes, s'aventurent le plus loin dans les ouvertures? Les juvéniles? Les oiseaux subordonnés?

2) Étant donné que le risque de mort par inanition varie pendant l'hiver, l'effet observé du couvert forestier sur la propension des mésanges à s'exposer au risque d'être victime de prédation varie-t-il d'un mois à l'autre, mais aussi à différentes latitudes?

3) De quelle manière les résultats seraient-ils influencés par une manipulation, non seulement de la quantité de nourriture disponible, mais aussi, de sa prédictibilité.

4) Les individus vivant dans les forêts les plus fragmentées sont-ils morphologiquement différents (p.ex. longueur relative des ailerons par rapport aux autres mesures corporelles) des individus présents dans les milieux plus intègres et donc, plus aptes (adaptation découlant des contraintes imposées par l'habitat: chez les adultes du moins, leur mue ayant eu lieu dans l'environnement immédiat) au vol en milieu ouvert (voir Swaddle et Witter 1998)?

Annexe A

1) Serait-il possible d'améliorer la technique d'inventaire proposée (p. ex. période de diffusion plus longue de l'enregistrement, pause entre deux séquences rapprochées de diffusion)?

2) De quelle manière le couvert forestier (p. ex. proportion de résineux, importance du couvert dans un rayon de quelques centaines de mètres) affecte-t-il l'efficacité de la diffusion des cris de houspillage et la réponse des oiseaux?

Bibliographie

- Aberg, J., J. E. Swenson, and H. Andrén. 2000. The dynamics of Hazel Grouse (*Bonasa bonasia* L.) occurrence in habitat fragments. *Canadian Journal of Zoology* 78: 352-358.
- Ahlborn, B., and R. W. Blake. 2001. Why birds cannot be smaller than bees. *Canadian Journal of Zoology* 79: 1724-1726.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.
- Anon. 1999. SAS Release 8.1. SAS Institute Inc, Cary.
- Anon. 2004. Canadian Climate Information. URL: <http://www.msc-smc.ec.gc.ca/climate/>.
- Austen, M. J. W., C. M. Francis, D. M. Burke, and M. S. W. Bradstreet. 2001. Landscape context and fragmentation effects on forest birds in southern Ontario. *Condor* 103:701-714.
- Bélisle, M., A. Desrochers, and M.-J. Fortin. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* 82: 1893-1904.
- Bent, A. C. 1946. Life histories of North American jays, crows, and titmice. U. S. National Museum Bulletin 191.
- Berger, M., and J. S. Hart. 1974. Physiology and energetics of flight. *Avian Biology* 4: 415-477.
- Blake, J. G. 1987. Species-area relationships of winter residents in isolated woodlots. *Wilson Bulletin* 99: 243-252.
- Blem, C. R. 1984. Ratios in avian physiology. *Auk* 101: 153-155.
- Blem, C. R. 1990. Avian energy storage. *Current ornithology* 7: 59-113.
- Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology: theory and applications. *Current Ornithology* 11: 35-91.
- Boulinier, T. et al. 2001. Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology* 82: 1159-1169.
- Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Canadian Journal of Zoology* 68: 203-220.
- Brand, L. A., and T. L. George. 2001. Response of passerine birds to forest edge in coast redwood forest fragments. *Auk* 118: 678-686.
- Brewer, D., A. Diamond, E. J. Woodsworth, B. T. Collins, and E. H. Dunn. 2000. Canadian atlas of bird banding. Vol. 1: Doves, cuckoos, and hummingbirds through passerines, 1921-1995. Environment Canada, Canadian Wildlife Service, Ottawa.
- Brittingham, M. C., and S. A. Temple. 1988. Impacts of supplemental feeding on survival rates of Black-capped Chickadees. *Ecology* 69: 581-589.
- Broggi, J., M. Orell, E. Hohtola, and J.-A. Nilsson. 2004. Metabolic response to temperature variation in the great tit: an interpopulation comparison. *Journal of Animal Ecology* 73: 967-972.
- Brodin, A. 2000. Why do hoarding birds gain fat in winter in the wrong way? Suggestions from a dynamic model. *Behavioral Ecology* 11: 27-39.
- Brodin, A., and C. W. Clark, 1997. Long-term hoarding in the Paridae: a dynamic model. *Behavioral Ecology* 8: 178-185.

- Brodin, A., and J. Ekman. 1994. Benefits of food hoarding. *Nature* 372: 510.
- Brotons, L., A. Desrochers, and Y. Turcotte. 2001. Food hoarding behaviour of black capped chickadees (*Poecile atricapillus*) in relation to forest edges. *Oikos* 95: 511-519.
- Brown, M. E. 1996. Assessing body condition in birds. *Current ornithology* 13: 67-135.
- Browning, M. R. 1995. Do Downy Woodpeckers migrate? *Journal of Field Ornithology* 66: 12-21.
- Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *Auk* 115: 96-104.
- Burnham, K. P., and D. R. Anderson. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* 28: 111-119.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edn. Springer-Verlag, New York.
- Calder, W. A. 1984. Size, function, and life history. Harvard University Press, Cambridge.
- Caraco, T. 1979. Time budgeting and group size: a test of theory. *Ecology* 60: 618-627.
- Caraco, T., S. Martindale, and H. R. Pulliam. 1980. Avian time budgets and distance to cover. *Auk* 97: 872-875.
- Carey, C., and W. R. Dawson. 1999. A search for environmental cues used by birds in survival of cold winters. *Current Ornithology* 15: 1-31.
- Carrascal, L. M., J. A. Diaz, D. L. Huertas, and I. Mozetich. 2001. Behavioral thermoregulation by Treecreepers: trade-off between saving energy and reducing crypsis. *Ecology* 82: 1642-1654.
- Chaplin, S. B. 1974. Daily energetics of the Black-capped Chickadee, *Parus atricapillus*, in winter. *Journal of Comparative Physiology B* 89: 321-330.
- Chaplin, S. B. 1976. The physiology of hypothermia in the Black-capped Chickadee, *Parus atricapillus*. *Journal of Comparative Physiology B* 112: 335-344.
- Clark, C. W., and J. Ekman. 1995. Dominant and subordinate fattening strategies: a dynamic game. *Oikos* 72: 205-212.
- Cooper, C. B., and J. R. Walters. 2002. Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. *Conservation Biology* 16: 471-478.
- Cooper, S. J. 1999. The thermal and energetic significance of cavity roosting in Mountain Chickadees and Juniper Titmice. *Condor* 101: 863-866.
- Cooper, S. J., and J. A. Gessaman. 2004. Thermoregulation and habitat preference in mountain chickadee and juniper titmice. *Condor* 106: 852-861.
- Cooper, S. J., and D. L. Swanson. 1994. Seasonal acclimatization of thermoregulation in the Black-capped Chickadee. *Condor* 96: 638-646.
- Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400: 563-566.
- De Laet, J. F. 1985. Dominance and anti-predator behaviour of Great Tits *Parus major*: a field study. *Ibis* 127: 372-377.
- Desrochers, A., M. Bélisle, and J. Bourque. 2002. Do mobbing calls affect the perception of predation risk by forest birds? *Animal Behaviour* 64: 709-714.
- Desrochers, A., S. J. Hannon, and K. E. Nordin. 1988. Winter survival and territory acquisition in a northern population of Black-capped Chickadees. *Auk* 105: 727-736.

- Doherty, P. F., Jr., and T. C. Grubb, Jr. 2000. Habitat and landscape correlates of presence, density, and species richness of birds wintering in forest fragments in Ohio. *Wilson Bulletin* 112: 388-394.
- Doherty, P. F., Jr., and T. C. Grubb, Jr. 2002. Survivorship of permanent-resident birds in a fragmented landscape. *Ecology* 83: 844-857.
- Doherty, P. F., Jr., and T. C. Grubb, Jr. 2003. Relationship of nutritional condition of permanent-resident woodland birds with woodlot area, supplemental food, and snow cover. *Auk* 120: 331-336.
- Dolby, A. S., and T. C. Grubb, Jr. 1999. Effects of winter weather on horizontal and vertical use of isolated forest fragments by bark-foraging birds. *Condor* 101: 408-412.
- Downes, C. M., et B. T. Collins. 2003. Le relevé des oiseaux nicheurs du Canada, de 1967 à 2000. Service canadien de la faune. Cahier de biologie No. 219.
- Dufour, K. W., and P. J. Weatherhead. 1991. A test of the condition-bias hypothesis using Brown-headed Cowbirds trapped during the breeding season. *Canadian Journal of Zoology* 69: 2686-2692.
- Dunn, E. H. 2001. Mass change during migration stopover: a comparison of species group and sites. *Journal of Field Ornithology* 72: 419-432.
- Dunn, E. H. 2002. A cross-Canada comparison of mass change in birds during migration stopover. *Wilson Bulletin* 114: 368-379.
- Ecoregion Working Group. 1989. Ecoclimatic regions of Canada, first approximation. *Ecol. Land Classif. Series 23*. Environment Canada, Ottawa.
- Elkie, P., R. Rempel, and A. Carr. 1999. Patch Analyst user's manual. TM-002. Ontario Ministry of Natural Resources, Northwest Science & Technology, Thunder Bay.
- Environment Canada. 2002. Canadian Climate and Water Information. URL: <http://www.msc-smc.ec.gc.ca/climate/>.
- Environment Canada. 2005. Canadian Climate Information. URL: http://www.climat.meteo.ec.gc.ca/climate_normals/.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61: 603-610.
- Fauchald, P., T. Tveraa, C. Henaug, and N. Yoccoz 2004. Adaptive regulation of body reserves in reindeer, *Rangifer tarandus*: a feeding experiment. *Oikos* 107: 583-591.
- Flather, C. H., and M. Bevers. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *American Naturalist* 159: 40-56.
- Frankino, W. A., B. J. Zwaan, D. L. Stern, and P. M. Brakefield. 2005. Natural selection and developmental constraints in the evolution of allometries. *Science* 307: 718-720.
- Freemark, K. E., and B. Collins. 1992. Landscape ecology of birds breeding in temperate forest fragments. In: *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan, III, and D. W. Johnston, eds.), pp. 443-454. Smithsonian Institution Press, Washington.
- Freemark, K. E., and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biological Conservation* 36: 115-141.

- Gibbs, J. P., and J. Faaborg. 1990. Estimating the viability of Ovenbird and Kentucky Warbler populations in forest fragments. *Conservation Biology* 4: 193-196.
- Gobeil, J.-F., and M.-A. Villard. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos* 98: 447-458.
- Gorney, E., W. S. Clark, and Y. Yom-Tov. 1999. A test of the condition-bias hypothesis yields different results for two species of sparrowhawks (*Accipiter*). *Wilson Bulletin* 111: 181-187.
- Gosler, A. G. 1996. Environmental and social determinants of winter fat storage in the great tit *Parus major*. *Journal of Animal Ecology* 65: 1-17.
- Graber, J. W., and R. R. Graber. 1979. Severe winter weather and bird populations in southern Illinois. *Wilson Bulletin* 91: 88-103.
- Graedel, S. K., and R. E. Loveland. 1995. Seasonal and diurnal mass variation in Black-capped Chickadees and White-throated Sparrows. *Wilson Bulletin* 107: 723-727.
- Graham, C. H. 2001. Factors influencing movement patterns of Keel-billed Toucans in a fragmented tropical landscape in southern Mexico. *Conservation Biology* 15: 1789-1798.
- Greenwood, J. G. 2003. Measuring sexual size dimorphism in birds. *Ibis* 145 (on-line): E124-E126.
- Grubb, T. C., Jr. 1977. Weather-dependent foraging behavior of some birds wintering in a deciduous woodland: horizontal adjustments. *Condor* 79: 271-274.
- Grubb, T. C., Jr. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. *Auk* 106: 314-320.
- Grubb, T. C., Jr., and P. F. Doherty, Jr. 1999. On home-range gap-crossing. *Auk* 116: 618-628.
- Grubb, T. C., Jr., and L. Greenwald. 1982. Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. *Animal Behaviour* 30: 637-640.
- Haila, Y. 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications* 12: 321-334.
- Haila, Y., D. A. Saunders, and R. J. Hobbs. 1993. What do we presently understand about ecosystem fragmentation? In: *Reconstruction of fragmented ecosystems: global and regional perspectives* (Saunders, D. A., R. J. Hobbs, and P. R. Ehrlich, eds.), pp. 45-55. Surrey Beatty and Sons, Chipping Norton.
- Hamel, P. B., W. P. Smith, and J. W. Wahl. 1993. Wintering bird populations of fragmented forest habitat in the Central Basin, Tennessee. *Biological Conservation* 66: 107-115.
- Hames, R. S., K. V. Rosenberg, J. D. Lowe, and A. A. Dhondt. 2001. Site reoccupation in fragmented landscapes: testing predictions of metapopulation theory. *Journal of Animal Ecology* 70: 182-190.
- Hanski, I. 1994. Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution* 9: 131-135.
- Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22: 225-232.
- Heinrich, B. 2003. Overwintering of Golden-crowned Kinglets during winter. *Wilson Bulletin* 115: 113-114.

- Hilton, G. M., W. Cresswell, and G. D. Ruxton. 1999. Intraflock variation in the speed of escape-flight response on attack by an avian predator. *Behavioral Ecology* 10: 391-395.
- Hinsley, S. A. 2000. The costs of multiple patch use by birds. *Landscape Ecology* 15: 765-775.
- Hinsley, S. A., P. E. Bellamy, and D. Moss. 1995. Sparrowhawk *Accipiter nisus* predation and feeding site selection by tits. *Ibis* 137: 418-420.
- Houston, A. I., and J. M. McNamara. 1993. A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scandinavica* 24: 205-219.
- Houston, A. I., J. M. McNamara, and J. M. C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society B* 341: 375-397.
- Huhta, E., J. Jokimäki, and P. Rahko. 1999. Breeding success of Pied Flycatchers in artificial forest edges: the effect of a suboptimally shaped foraging area. *Auk* 116: 528-535.
- Hurd, C. R. 1996. Interspecific attraction to the mobbing calls of Black-capped Chickadees (*Parus atricapillus*). *Behavioural Ecology and Sociobiology* 38: 287-292.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187-211.
- Imbeau, L., and A. Desrochers. 2002. Foraging ecology and use of drumming trees by Three-toed Woodpeckers. *Journal of Wildlife Management* 66: 222-231.
- Imbeau, L., J.-P. Savard, and R. Gagnon. 1999. Comparing bird assemblages in successional black spruce stands originating from fire and logging. *Canadian Journal of Zoology* 77: 1850-1860.
- Jansson, C., J. Ekman, and A. von Brössen. 1981. Winter mortality and food supply in tits *Parus* spp. *Oikos* 37: 313-322.
- Kaiser, A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. *Journal of Field Ornithology* 64: 246-255.
- Kallander, H., and H. G. Smith. 1990. Food storing in birds: an evolutionary perspective. *Current Ornithology* 7: 147-207.
- Karr, J. R., J. D. Nichols, M. K. Klimkiewicz, and J. D. Brawn. 1990. Survival rates of birds of tropical and temperate forests: will the dogma survive? *American Naturalist* 136: 277- 291.
- Koenig, W. D., and J. M. H. Knops. 2001. Seed-crop size and eruptions of North American boreal seed-eating birds. *Journal of Animal Ecology* 70: 609-620.
- Koivula, K., M. Orell, and K. Lahti. 2002. Plastic daily fattening routines in willow tits. *Journal of Animal Ecology* 71: 816-823.
- Kolozsvary, M. B., and R. K. Swihart. 1999. Habitat fragmentation and the distribution of amphibians: patch and landscape correlates in farmland. *Canadian Journal of Zoology* 77: 1288-1299.
- Krams, I. 2002. Mass-dependent take-off ability in wintering great tits (*Parus major*): comparison of top-ranked adult males and subordinate juvenile females. *Behavioral Ecology and Sociobiology* 51: 345-349.
- Kullberg, C., S. Jakobsson, and T. Fransson. 2000. High migratory fuel loads impair predator evasion in sedge warblers. *Auk* 117: 1034-1038.
- Lahti, K., M. Orell, S. Rytönen, and K. Koivula. 1998. Time and food dependence in willow tit winter survival. *Ecology* 79: 2904-2916.

- Lee, M., L. Fahrig, K. Freemark, and D. J. Currie. 2002. Importance of patch scale vs landscape scale on selected forest birds. *Oikos* 96: 110-118.
- Lehikoinen, E. 1987. Seasonality of the daily weight cycle in wintering passerines and its consequences. *Ornis Scandinavica* 18: 216-226.
- Liknes, E. T., S. M. Scott, and D. L. Swanson. 2002. Seasonal acclimatization in the America Goldfinch revisited: to what extent do metabolic rates vary seasonally? *Condor* 104: 548-557.
- Lilliendahl, K. (2002) Daily patterns of body mass gain in four species of small wintering birds. *Journal of Avian Biology*, **33**, 212-218.
- Lima, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia* 66: 60-67.
- Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67: 377-385.
- Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist* 153: 649-659.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619-640.
- Lind, J., T. Fransson, S. Jakobsson, and C. Kullberg. 1999. Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. *Behavioral Ecology and Sociobiology* 46: 65-70.
- Loery, G. and Nichols, J. D. 1985. Dynamics of a Black-capped Chickadee population, 1958-1983. *Ecology* 66: 1195-1203.
- Loery, G., K. H. Pollock, J. D. Nichols, and J. E. Hines. 1987. Age-specificity of Black-capped Chickadee survival rates: analysis of capture-recapture data. *Ecology* 68: 1038-1044.
- Machtans, C. S., M.-A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. *Conservation Biology* 10: 1366-1379.
- Macleod, R., P. Barnett, J. A. Clark, and W. Cresswell. 2005. Body mass change strategies in blackbirds *Turdus merula*: the starvation-predation risk trade-off. *Journal of Animal Ecology* 74: 292-302.
- Matthysen, E. 1990. Nonbreeding social organization in *Parus*. *Current Ornithology* 7: 209-249.
- Matthysen, E. 1993. Nonbreeding social organization in migratory and resident birds. *Current Ornithology* 11: 93-141.
- Matthysen, E. 1999. Nuthatches (*Sitta europaea*: Aves) in forest fragments: demography of a patchy population. *Oecologia* 119: 501-509.
- McKechnie, A. E., and B. G. Lovegrove. 2002. Avian facultative hypothermic responses: a review. *Condor* 104: 705-724.
- McNamara, J. M., and A. I. Houston. 1980. The application of statistical decision theory to animal behaviour. *Journal of Theoretical Biology* 85: 673-690.
- McNamara, J. M., and A. I. Houston. 1990. The value of fat reserves and the trade-off between starvation and predation. *Acta Biotheoretica* 38: 37-61.
- McNamara, J. M., J. Ekman, and A. I. Houston. 2004. The effect of thermoregulatory substitution on optimal energy reserves of small birds in winter. *Oikos* 105: 192-196.

- McNamara, J. M., A. I. Houston, and J. R. Krebs. 1990. Why hoard? The economics of food storing in tits, *Parus* spp. *Behavioral Ecology* 1: 12-23.
- McNamara, J. M., A. I. Houston, and S. L. Lima. 1994. Foraging routines of small birds in winter: a theoretical investigation. – *Journal of Avian Biology* 25: 287-302.
- Merom, K., Y. Yom-Tov, and R. McClery. 2000. Philopatry to stopover site and body condition of transient reed warblers during autumn migration through Israël. *Condor* 102: 441-444.
- Metcalfe, N. B., and S. E. Ure. 1995. Diurnal variation in flight performance and hence potential predation risk in small birds. *Proceedings of the Royal Society of London B* 261: 395-400.
- Middleton, A. L. A. 1986. Seasonal changes in plumage structure and body composition of the American Goldfinch, *Carduelis tristis*. *Canadian Field-Naturalist* 100: 545-549.
- Pennycuik, C. J. 1989. Bird flight performance: a practical calculation manual. Oxford University Press, Oxford.
- Perkins, A. L., W. R. Clark, T. Z. Riley, and P. A. Vohs. 1997. Effects of landscape and weather on winter survival of Ring-necked Pheasant hens. *Journal of Wildlife Management* 61: 634-644.
- Pimm, S. L. 1998. The forest fragment classic. *Nature* 393: 23-24
- Pravosudov, V. V., and T. C. Grubb, Jr. 1997a. Energy management in passerine birds during the nonbreeding season. *Current ornithology* 14: 189-234.
- Pravosudov, V. V., and T. C. Grubb, Jr. 1997b. Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food supply. *Behavioral Ecology* 8: 332-339.
- Pravosudov, V. V., and T. C. Grubb, Jr. 1998a. Management of fat reserves in tufted titmice *Baeolophus bicolor* in relation to risk of predation. *Animal Behaviour* 56: 49-54.
- Pravosudov, V. V., and T. C. Grubb, Jr. 1998b. Management of fat reserves in tufted titmice (*Parus bicolor*): evidence against a trade-off with food hoards. *Behavioral Ecology and Sociobiology* 42: 57-62.
- Pravosudov, V. V., and J. R. Lucas. 2001. A dynamic model of short-term energy management in small food-caching and non-caching birds. *Behavioral Ecology* 12: 207-218.
- Pulliam, H. R. 1973. On the advantages of flocking. *Journal of Theoretical Biology* 38: 418-422.
- Pyle, P. 1997. Identification guide to North American birds. Part 1. Columbidae to Ploceidae. Slate Creek Press, Bolinas.
- Redfern, C. P. F., A. E. J. Slough, B. Dean, J. L. Brice, and P. H. Jones 2000. Fat and body condition in migrating redwings *Turdus iliacus*. *Journal of Avian Biology* 31: 197-205.
- Ressources naturelles et Faune. 2005. Règlement sur les normes d'intervention dans les forêts du domaine de l'État. Loi sur les forêts. Éditeur officiel du Québec, Québec.
- Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the neotropics. *Proceedings of the National Academy of Sciences* 86: 7658-7662.

- Robinson, S. K., F. R. Thompson, III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267: 1987-1990.
- Rodewald, A. D., and R. H. Yahner. 2001. Influence of landscape composition on avian community structure and associated mechanisms. *Ecology* 82: 3493-3504.
- Rodriguez, A., H. Andrén, and G. Jansson. 2001. Habitat-mediated predation risk and decision making of small birds at forest edges. *Oikos* 95: 383-396.
- Rogers, C. M. 2003. New and continuing issues with using visible fat classes to estimate fat stores of birds. *Journal of Avian Biology* 34: 129-133.
- Rogers, C. M., and R. Heath-Coss. 2003. Effect of experimentally altered food abundance on fat reserves of wintering birds. *Journal of Animal Ecology* 72: 822-830.
- Rogers, C. M., and J. N. M. Smith. 1993. Life-history theory in the non-breeding period: trade-offs in avian fat reserves. *Ecology* 74: 419-426.
- SAS Institute Inc. 1999. SAS Release 8.1. SAS Institute Inc, Cary.
- Schmidt, K. A. 2003. Nest predation and population declines in Illinois songbirds: a case for mesopredator effects. *Conservation Biology* 17: 1141-1150.
- Schmiegelow, F. K. A., and M. Mönkkönen. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecological Applications* 12: 375-389.
- Schneider, K. J. 1984. Dominance, predation, and optimal foraging in White-throated Sparrow flocks. *Ecology* 65: 1820-1827.
- Schultz, E. T., and D. O. Conover. 1999. The allometry of energy reserve depletion: test of a mechanism for size-dependent winter mortality. *Oecologia* 119: 474-483.
- Shettleworth, S. J., R. R. Hampton, and R. P. Westwood. 1995. Effects of season and photoperiod on food storing by black-capped chickadees, *Parus atricapillus*. *Animal Behaviour* 49: 989-998.
- Smith, S. M. 1984. Flock switching in chickadees: why be a winter floater? *American Naturalist* 123: 81-98.
- Smith, S. M. 1991. *The Black-capped Chickadee: behavioral ecology and natural history*. Cornell University Press, Ithaca.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. 2nd edn. Freeman, San Francisco.
- Stephens, P. A., S. W. Buskirk, G. D. Hayward, and C. Martinez Del Rio. 2005. Information theory and hypothesis testing: a call for pluralism. *Journal of Applied Ecology* 42: 4-12.
- Stokes, M. E., C. S. Davis, and G. G. Koch. 2000. *Categorical data analysis using the SAS system*. 2nd edn. SAS Institute Inc., Cary.
- Swaddle, J. P. and Witter, M. S. 1998. Cluttered habitats reduce wing asymmetry and increase flight performance in European starlings. *Behavioral Ecology and Sociobiology* 42: 281-287.
- Swanson, D. L. 1990. Seasonal variation of cold hardiness and peak rates of cold-induced thermogenesis in the Dark-eyed Junco (*Junco hyemalis*). *Auk* 107: 561-566.
- Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68: 571-573.
- Telleria, J. L. and Santos, T. 1995. Effects of forest fragmentation on a guild of wintering passerines: the role of habitat selection. *Biological Conservation* 71: 61-67.

- Telleria, J. L., E. Virgos, R. Carbonell, J. Pérez-Tris, and T. Santos 2001. Behavioural responses to changing landscapes: flock structure and anti-predator strategies of tits wintering in fragmented forests. *Oikos* 95: 253-264.
- Terborgh, J. W. 1989. *Where have all the birds gone?* Princeton University Press, Princeton.
- Thompson, F. R. III, and E. K. Fritzell. 1988. Ruffed Grouse winter roost site preference and influence on energy demands. *Journal of Wildlife Management* 52: 454-460.
- Turcotte, Y., and A. Desrochers. 2002. Playbacks of mobbing calls of Black-capped Chickadees help estimate the abundance of forest birds in winter. *Journal of Field Ornithology* 73: 303-307.
- Turcotte, Y., and A. Desrochers. 2003. Landscape-dependent response to predation risk by forest birds. *Oikos* 100: 614-618.
- Turcotte, Y., and A. Desrochers. 2005. Landscape-dependent distribution of northern forest birds in winter. *Ecography* 28: 129-140.
- Van Wilgenburg, D. F. Mazerolle, and K. A. Hobson. 2001. Patterns of arthropod abundance, vegetation, and microclimate at boreal forest edge and interior in two landscapes: implications for forest birds. *Écoscience* 8: 454-461.
- Villard, M.-A., P. R. Martin, and C. G. Drummond. 1993. Habitat fragmentation and the pairing success in the Ovenbird (*Seiurus aurocapillus*). *Auk* 110: 759-768.
- Villard, M.-A., M. K. Trzcinski, and G. Merriam. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology* 13: 774-783.
- Wallace, G. J. 1941. Winter studies of color-banded chickadees. *Bird-Banding* 12: 49-67.
- Walsberg, G. E. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. *Auk* 103: 1-7.
- Walther, B. A., and A. G. Gosler. 2001. The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (*Aves: Parus*). *Oecologia* 129: 312-320.
- Weise, C. M., and J. R. Meyer. 1979. Juvenile dispersal and development of site-fidelity in the Black-capped Chickadee. *Auk* 96: 40-55.
- Weatherhead, P. J., and H. Greenwood. 1981. Age and condition bias of decoy-trapped birds. *Journal of Field Ornithology* 52: 10-15.
- Whitcomb, R. F., J. F. Lynch, M. K. Klimkiewicz, C. S. Robbins, B. L. Whitcomb, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. In: *Forest island dynamics in man-dominated landscapes* (R. L. Burgess, and D. M. Sharpe, eds.), pp. 125-205. Springer-Verlag, New York.
- Wilson, W. H., Jr. 2001. The effects of supplemental feeding on wintering Black-capped Chickadees (*Poecile atricapilla*) in central Maine: population and individual responses. *Wilson Bulletin* 113: 65-72.
- Winker, K. 1995. Autumn stopover on the isthmus of Tehuantepec by woodland Nearctic-Neotropical migrants. *Auk* 112: 690-700.
- Winker, K., D. W. Warner, and A. R. Weisbrod. 1992. Daily mass gains among woodland migrants at an island stopover site. *Auk* 109: 853-862.
- Witter, M. S., and I. E. Cuthill. 1993. The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London B* 340: 73-90.

- Yong, W., and F. R. Moore. 1993. Relation between migratory activity and energetic condition among thrushes (Turdinae) following passage across the Gulf of Mexico. *Condor* 95: 934-943.
- Zanette, L., P. Doyle, and S. M. Trémont. 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* 81: 1654-1666.
- Zanette, L. 2001. Indicators of habitat quality and the reproductive output of a forest songbird in small and large fragments. *Journal of Avian Biology* 32: 38-46.

Annexe A: Playbacks of mobbing calls of Black-capped Chickadees help estimate the abundance of forest birds in winter

Avertissement

Le contenu de la présente annexe a été publié à l'été de 2002. Hormis quelques changements mineurs dans le format ayant été nécessaires à la préparation de la thèse, le lecteur trouvera ici toute l'information contenue dans :

Turcotte, Y, and A. Desrochers. 2002. Playbacks of mobbing calls of Black-capped Chickadees help estimate the abundance of forest birds in winter. *Journal of Field Ornithology* 73: 303-307.

Résumé

Beaucoup d'efforts ont été investis dans le développement de méthodes permettant d'évaluer de manière précise les effectifs des populations d'oiseaux forestiers en période de nidification. Cependant, beaucoup moins nombreuses ont été les études visant à développer des méthodes applicables en dehors de cette période lorsque l'activité vocale des oiseaux est minimale et que ceux-ci ne sont plus territoriaux. Nous avons évalué une nouvelle approche utilisable pour les inventaires des oiseaux forestiers devant être effectués pendant l'hiver, soit l'utilisation d'un enregistrement de cris de houspillage de la Mésange à tête noire (*Poecile atricapilla*). La diffusion de ce type d'enregistrement lors des points d'écoute permettait la détection de plus d'individus, toutes espèces confondues et de plus d'espèces, que lorsque ce type d'enregistrement n'était pas utilisé. En cette période de l'année, l'heure du jour n'avait pas d'effet sur les résultats des inventaires, que l'enregistrement soit diffusé ou non. En raison de leur efficacité, nous recommandons l'utilisation de tels enregistrements lors des inventaires d'oiseaux forestiers devant être conduits en dehors de la période de nidification.

Abstract

Considerable attention has been devoted to the technical aspects of terrestrial bird surveys during the breeding season. However, there is a paucity of information specifically addressing the methodology of bird surveys at other times of the year when birds are less vocal and are mobile over areas larger than territories. We tested a method for surveying forest birds in winter, based on the use of playbacks of mobbing calls of Black-capped Chickadees (*Poecile atricapilla*). When compared to pre-playback 5 min standard point counts, playbacks of mobbing calls of the same duration allowed the detection of more individuals and more species. Time of day, with or without playbacks, had no effect on the number of individuals detected nor on species richness. We recommend the use of playbacks of mobbing calls of Black-capped Chickadees for surveying forest birds during the non-breeding season because of their efficiency.

Introduction

Considerable attention has been devoted in the past to the methodological aspects of terrestrial bird surveys during the breeding season (e.g., Ralph and Scott 1981, Ralph et al. 1995). The intense territorial singing activity of males then represents a key source of information to estimate population numbers. However, much less information is available concerning census procedures for the non-breeding season. During winter, birds are less vocal and dwell over areas larger than territories. Therefore, a well-proven method such as the fixed-radius point count conceived to survey birds during the breeding season becomes inefficient (e.g., Fletcher et al. 2000). Other survey approaches such as unlimited distance point counts (e.g., Gutzwiller 1991), transects (e.g., Rollfinke and Yahner 1990) or mapping (e.g., Smith 1984) have been used during the non-breeding season but each of these also presents some limitations (see Verner 1985). This situation may be in part responsible for the relative paucity of bird community studies conducted in winter, despite the critical importance of this time of year on bird survival (e.g., Desrochers et al. 1988, Lahti et al. 1998).

In this paper we propose a new method for surveying resident forest bird communities in winter. This method relies on the use of playbacks of mobbing calls of Black-capped Chickadees (*Poecile atricapilla*). During winter, the Black-capped Chickadee is the most abundant non-irruptive forest bird species in our study area as well as over much of the northern part of North America. Its mobbing calls are given year round (Shedd 1983) and are known to communicate the presence of predators to conspecifics as well as to other species (mostly passerines; Hurd 1996) that whenever present, quickly aggregate around a mobbing bird, often joining it in mobbing. For this reason, playbacks of mobbing calls of Black-capped Chickadees have already been used with success in different situations (e.g., Desrochers and Hannon 1997, Gunn et al. 2000). The innovative aspect of the new census method proposed is that the species targeted are not only those broadcast on playbacks as it is normally the case (e.g., Falls 1981, Gibbs and Melvin 1993), but rather a large proportion of those present in the community. To evaluate the value of this approach, we compared the results obtained in counts during which we used playbacks of mobbing calls of Black-capped Chickadees with those of fixed-radius standard point counts.

Study area and methods

Surveys were conducted on the south shore of the St. Lawrence River estuary, in Kamouraska County, Quebec, Canada (47° 30' N, 69° 50' W). The study area covered approximately 600 km² of agricultural landscape where forest vegetation is dominated by Balsam Fir (*Abies balsamea*), Quaking Aspen (*Populus tremuloides*), White Spruce (*Picea glauca*) and Paper Birch (*Betula papyrifera*). Based on a LANDSAT-7 satellite image taken in August 1999 and analyzed with Patch Analyst (Elkie et al. 1999), forest cover within 250 m of the center of the census sites ranges from 12 to 92%.

We conducted bird surveys at different times of day from sunrise to sunset, from November to February during 3 consecutive winters (1998-1999 to 2000-2001) in 24 census sites. These sites were selected in the context of a larger study of Black-capped Chickadee winter ecology along a gradient of forest fragmentation. Census sites were separated from each other by at least 2 km. The center of each census site was located at the intersection of a forest, a field and a tertiary road. This type of roadside location is presumed to increase detection rates, particularly of silent flying birds (Ralph et al. 1995). The observer (YT) stood in the field about 10 m from the center of the census site while an assistant took note of all birds seen or heard within a fixed-radius of 50 m. Birds flying above the forest were not considered. Surveys were not conducted during heavy precipitations or when peak wind speed, measured 1.5 m above ground with a hand-held anemometer, exceeded 30 km/h as hearing ability then becomes limited and probability of detection decreases.

At each site, we used back-to-back two types of counts. We began with a 5 min standard point count period (hereafter, pre-playback). It was immediately followed by another 5 min point count period during which we playbaked mobbing calls of Black-capped Chickadees (hereafter, playback). The mobbing chickadees were recorded with a parabola near Quebec City when lured by a stuffed Screech Owl (*Otus asio*). Calls were playbaked with a 5 W amplifier facing skyward, attached to a cassette player and placed on the ground at the center of the census site. On days without wind, we were able to hear this recording from as far away as about 200 m in the open. Sound level measured 1 m above the amplifier with a sound level meter (RealisticTM) reached 105 decibels.

As each of the 24 census sites was surveyed 3 to 7 times within this period (no more than one survey per month), data were averaged per site, in order to avoid pseudoreplication. To test the hypothesis that playbacks resulted in higher counts, we used Wilcoxon Signed-Ranks tests, appropriate for a paired comparisons design. Since the alternative hypothesis was that playbacks increase the number of birds detected, tests were one-tailed. To evaluate the effect of time of day on species richness and total number of individuals detected in the surveys, we analyzed count results as a repeated-measures design with a Poisson regression. We carried out statistical analysis using SAS (SAS Institute Inc. 1999).

Results

Comparison of pre-playback and playback counts

Playbacks allowed us to detect more species, more individuals (all species combined) and more Black-capped Chickadees (about 75% of all individuals detected) than did pre-playback counts (Table 1). We also tested the effect of playbacks on species other than Black-capped Chickadees that were present during the surveys. To reduce the risk of type II statistical errors while performing analyses at the species level, we excluded species that were present in less than 5 (20%) of the census sites (13 out of the 18 species recorded, Table 2). Playbacks provided more observations of Golden-crowned Kinglet (*Regulus satrapa*), Blue Jay (*Cyanocitta cristata*), and Downy Woodpecker (*Picoides pubescens*) but not of Hairy Woodpecker (*Picoides villosus*) (Table 1).

Table 1. Mean (\pm SE) species richness and number of individuals of the most commonly detected species during paired pre-playback and playback counts (5 min duration, 50 m fixed-radius) within an agricultural landscape in Quebec during three consecutive winters, 1998-1999 to 2000-2001. Each census site ($n = 24$) was surveyed 3 to 7 times, but data were averaged for each site before analysis. Type of count effects on species richness and number of individuals were analyzed with one tailed Wilcoxon Signed-Ranks tests.

	Type of count		P
	Pre-playback	Playback	
Species richness	0.29 \pm 0.07	1.25 \pm 0.11	<0.0001
Black-capped Chickadee	0.34 \pm 0.10	3.63 \pm 0.46	<0.0001
Golden-crowned Kinglet	0.07 \pm 0.03	0.23 \pm 0.07	0.006
Blue Jay	0	0.13 \pm 0.06	0.004
Downy Woodpecker	0	0.05 \pm 0.02	0.031
Hairy Woodpecker	0.01 \pm 0.01	0.04 \pm 0.02	0.218
Total number of individuals	0.45 \pm 0.13	4.73 \pm 0.57	<0.0001

Table 2. Number of census sites (out of the 24 of this study) where each species was detected depending on the type of count.

Species	Type of count		
	Pre-playback	Playback	Total
Black-capped Chickadee (<i>Poecile atricapilla</i>)	15	24	24
Golden-crowned Kinglet (<i>Regulus satrapa</i>)	5	11	13
Blue Jay (<i>Cyanocitta cristata</i>)	0	8	8
Downy Woodpecker (<i>Picoides pubescens</i>)	0	5	5
Hairy Woodpecker (<i>Picoides villosus</i>)	1	4	5
Boreal Chickadee (<i>Poecile hudsonica</i>)	0	4	4
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	0	4	4
Pine Grosbeak (<i>Pinicola enucleator</i>)	0	2	2
Brown Creeper (<i>Certhia americana</i>)	0	2	2
Common Redpoll (<i>Carduelis flammea</i>)	0	2	2
American Goldfinch (<i>Carduelis tristis</i>)	0	1	1
Common Raven (<i>Corvus corax</i>)	0	1	1
Gray Jay (<i>Perisoreus canadensis</i>)	0	1	1
Northern Shrike (<i>Lanius excubitor</i>)	0	1	1
Pine Siskin (<i>Carduelis pinus</i>)	0	1	1
Three-toed Woodpecker (<i>Picoides tridactylus</i>)	1	1	1
Evening Grosbeak (<i>Coccothraustes vespertinus</i>)	1	0	1
Mourning Dove (<i>Zenaida macroura</i>)	1	0	1

Effect of time of day

There were no interactions between effects of count type and time of day whether species richness ($P = 0.42$) or total number of individuals ($P = 0.50$) was considered as the dependent variable. Therefore, irrespective of the type of count, time of day had no effect on species richness nor on total number of individuals detected (Table 3).

Table 3. Mean (\pm SE) species richness and total number of individuals during paired pre-playback and playback counts (5 min duration, 50 m fixed-radius) at different times of day (EST) within an agricultural landscape in Quebec during three consecutive winters, 1998-1999 to 2000-2001. Sample size refers to the number of census sites (out of the 24 of this study) that were surveyed in each time of day category. There were no interactions between effects of count type and time of day whether species richness or the total number of individuals was considered as the dependent variable. Time of day effects on species richness and total number of individuals results were analyzed with a repeated measures design with a Poisson regression.

Time of day	<i>n</i>	Species richness ^a		Total number of individuals ^b	
		Pre-playback	Playback	Pre-playback	Playback
Sunrise to 1000 h	18	0.23 \pm 0.09	1.19 \pm 0.19	0.26 \pm 0.10	4.74 \pm 1.07
1000-1200 h	20	0.28 \pm 0.11	1.38 \pm 0.20	0.50 \pm 0.23	5.22 \pm 1.05
1200-1400 h	20	0.31 \pm 0.11	1.03 \pm 0.17	0.56 \pm 0.25	3.16 \pm 0.86
1400 h to sunset	19	0.13 \pm 0.07	0.88 \pm 0.18	0.13 \pm 0.07	3.13 \pm 0.71

^a $P = 0.35$.

^b $P = 0.32$.

Discussion

The large amount of bird records that can be obtained efficiently by the use of playbacks of mobbing calls of Black-capped Chickadees represents its main advantage. Indeed, not only can it be used for the detection of individuals belonging to the mobbing species but also for what seems to represent a large proportion (if not the majority) of the birds and species present on a site (this study, Hurd 1996, Gunn et al. 2000). Playbacks could be particularly useful for the detection of rarer or more secretive species all year round. As Gunn et al. (2000) suggested, mobbing calls from another species (e.g., Carolina Chickadee (*Poecile carolinensis*) or White-breasted Nuthatch (*Sitta carolinensis*)) would probably be as effective in regions where Black-capped Chickadees are rare or absent.

Furthermore, results of playbacks (and of pre-playbacks as well) were not affected by time of day. This suggests that the use of mobbing calls does not need to be restricted to the early part of day as it is recommended for surveys conducted during the breeding season (e.g., Ralph et al. 1993). However, pre-playback results are in contradiction with those obtained in milder winter conditions by Rollfinke and Yahner (1990) who did fixed-width transects in Pennsylvania (ca. 40°N) and by Gutzwiller (1991) who conducted unlimited-distance point counts in Texas (ca. 31°N). Sampling throughout the day as we did, both of their studies found that observed species richness was associated with time of day. Rollfinke and Yahner (1990) also found that the total number of individuals was associated with time of day (not tested by Gutzwiller 1991).

Despite the efficiency of the above playback method, its use by different researchers or managers would probably yield less comparable results than those obtained by standard point counts. Indeed, broadcasting equipment or recordings will obviously always present differences of power or quality, associated with variation in the distance from which birds are lured. Therefore, we recommend that playback counts should be preceded by standard point counts in order to allow possible comparisons in time or space. Nevertheless, we consider that the use of playbacks of mobbing calls for forest bird surveys conducted outside the breeding season represents an efficient tool, particularly for species that are uncommon or hard to detect.

Literature cited

- Desrochers, A., and S. J. Hannon. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* 11: 1204-1210.
- Desrochers, A., S. J. Hannon, and K. E. Nordin. 1988. Winter survival and territory acquisition in a northern population of Black-capped Chickadees. *Auk* 105: 727-736.
- Elkie, P., R. Rempel, and A. Carr. 1999. Patch Analyst user's manual. TM-002. Ontario Ministry of Natural Resources, Northwest Science & Technology, Thunder Bay.
- Falls, J. B. 1981. Mapping territories with playback: an accurate census method for songbirds. *Studies in Avian Biology* 6: 86-91.
- Fletcher, R. J., Jr, J. A. Dhundale, and T. F. Dean. 2000. Estimating non-breeding season bird abundance in prairies: a comparison of two survey techniques. *Journal of Field Ornithology* 71: 321-329.
- Gibbs, J. P., and S. M. Melvin 1993. Call-response surveys for monitoring breeding waterbirds. *Journal of Wildlife Management* 57: 27-34.
- Gunn, J. S., A. Desrochers, M.-A. Villard, J. Bourque, and J. Ibarzabal. 2000. Playbacks of mobbing calls of Black-capped Chickadees as a method to estimate reproductive activity of forest birds. *Journal of Field Ornithology* 71: 472-483.
- Gutzwiller, K. J. 1991. Estimating winter species richness with unlimited-distance point count. *Auk* 108: 853-862.
- Hurd, C. R. 1996. Interspecific attraction to the mobbing calls of Black-capped Chickadees (*Parus atricapillus*). *Behavioural Ecology and Sociobiology* 38: 287-292.
- Lahti, K., M. Orell, S. Rytönen, and K. Koivula. 1998. Time and food dependence in Willow Tit winter survival. *Ecology* 79: 2904-2916.
- Ralph, C. J., and J. M. Scott, eds. 1981. Estimating numbers of terrestrial birds. *Studies in Avian Biology* No. 6.
- Ralph, C. J., S. Droege, and J. R. Sauer. 1995. Managing and monitoring birds using point counts: standards and applications. In: *Monitoring bird populations by point counts*. (C. J. Ralph, J. R. Sauer, and S. Droege, eds.), pp.161-168. General Technical Report PSW-GTR-149. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. General Technical Report PSW-GTR-144. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany.
- Rollfinke, B. F., and R. H. Yahner. 1990. Effects of time of day and season on winter bird counts. *Condor* 92: 215-219.
- SAS Institute Inc. 1999. SAS Release 8.1. SAS Institute Inc., Cary.
- Shedd, D. H. 1983. Seasonal variation in mobbing intensity in the Black-capped Chickadee. *Wilson Bulletin* 95: 343-348.
- Smith, P. G. R. 1984. Observer and annual variation in winter bird population studies. *Wilson Bulletin* 96: 561-574.
- Verner, J. 1985. Assessment of counting techniques. *Current Ornithology* 2: 247-302.