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Research Papers

Spatial Aggregation of Forest Songbird Territories and Possible Implications for Area Sensitivity

Agrégation spatiale des territoires d'oiseaux forestiers et influence possible sur la sensibilité à la superficie d'habitat

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ABSTRACT. Habitat area requirements of forest songbirds vary greatly among species, but the causes of this variation are not well understood. Large area requirements could result from advantages for certain species when settling their territories near those of conspecifics. This phenomenon would result in spatial aggregations much larger than single territories. Species that aggregate their territories could show reduced population viability in highly fragmented forests, since remnant patches may remain unoccupied if they are too small to accommodate several territories. The objectives of this study were twofold: (1) to seek evidence of territory clusters of forest birds at various spatial scales, lags of 250-550 m, before and after controlling for habitat spatial patterns; and (2) to measure the relationship between spatial autocorrelation and apparent landscape sensitivity for these species. In analyses that ignored spatial variation of vegetation within remnant forest patches, nine of the 17 species studied significantly aggregated their territories within patches. After controlling for forest vegetation, the locations of eight out of 17 species remained significantly clustered. The aggregative pattern that we observed may, thus, be indicative of a widespread phenomenon in songbird populations. Furthermore, there was a tendency for species associated with higher forest cover to be more spatially aggregated [ERRATUM].

RÉSUMÉ. La superficie d'habitat dont les oiseaux chanteurs forestiers ont besoin varie grandement selon les espèces, mais les causes de cette variation sont encore méconnues. Le besoin de grandes superficies d'habitat pourrait être lié aux avantages que retirent certaines espèces de l'établissement de leur territoire près de celui d'individus conspécifiques. Ce phénomène entraînerait des agrégations couvrant une superficie beaucoup plus grande que celle d'un territoire unique. La viabilité des populations d'espèces qui regroupent leurs territoires pourrait être réduite dans les forêts très fragmentées étant donné que les parcelles restantes peuvent demeurer inoccupées si elles sont trop petites pour permettre l'établissement de plusieurs territoires. La présente étude vise un double objectif : 1) chercher des indications de regroupements de territoires d'oiseaux forestiers à diverses échelles spatiales, avec des classes de distance de 250-550 m, avant et après avoir tenu compte de la structure spatiale de l'habitat; 2) mesurer la relation entre l'autocorrélation spatiale et la sensibilité apparente au paysage chez ces espèces. Dans les analyses qui ne tenaient pas compte de la structure spatiale de la végétation dans les parcelles de forêt restantes, neuf des 17 espèces étudiées regroupaient significativement leurs territoires dans les parcelles. Lorsque l'on a tenu compte de la végétation forestière, les territoires de huit espèces sur 17 sont demeurés significativement regroupés. Le type de regroupement que nous avons observé pourrait donc être indicatif d'un phénomène très répandu chez les populations d'oiseaux chanteurs. De plus, il y avait une forte tendance à l'autocorrélation spatiale chez les espèces influencées par le couvert forestier environnant.

Key Words: *spatial autocorrelation; forest fragmentation; landscape structure; migrant songbirds*

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INTRODUCTION

Forest songbird distribution is usually considered to depend on forest structure and composition at different spatial scales (McGarigal and McComb 1995, Hagan et al. 1997, Schmiegelow et al. 1997, Penhollow and Stauffer 2000). However, several factors could have an additional effect on avian distribution. For example, noncolonial species will sometimes settle their territories preferentially near conspecifics (Alatalo et al. 1982, Smith and Peacock 1990, Reed and Dobson 1993, Lima and Zollner 1996, Muller et al. 1997). This behavior may confer advantages in predator detection (Kenward 1978, Bildstein 1983, Stephens and Sutherland 1999, Perry and Andersen 2003) and greater opportunities in extra-pair mating (Wagner 1997, Norris and Stutchbury 2001, Mennill et al. 2004, Tarof et al. 2005). Alternatively, individuals may use the presence or reproductive performance of conspecifics to assess habitat quality when selecting a territory (Kiester and Slatkin 1974, Smith and Peacock 1990, Reed and Dobson 1993, Stamps 1987, 1988, 1994, 2001, Doligez et al. 2004*a*, Doligez et al. 2004*b*, Ward and Schlossberg 2004).

Loose aggregates of individual territories could be created within contiguous forests in species that prefer to settle near conspecifics. However, the generality of this phenomenon has yet to be demonstrated in forest birds. Indeed, most of the research on territorial aggregations has been conducted on a few well-studied species that tend to occur in high-density populations (e.g. Collared Flycatchers [*Ficedula albicollis*] Doligez et al. 1999, Pärt and Doligez 2003, Doligez et al. 2004*a*, *b*). In this paper, we examined how widespread territorial aggregations are by studying 17 forest bird species at various spatial scales, i.e., lags of 250-550 m. A general absence of aggregative behavior would suggest that clustering is a limited phenomenon in forest bird species. When found, territorial aggregations may simply be indicative of aggregations in habitat variables or other features. Thus, we also measured the contribution of vegetation structure on avian aggregative behavior.

Relatively few studies have incorporated spatial structure when studying the distribution of forest birds (Brown et al. 1995, Drolet et al. 1999, Koenig 1998, 2001, Lichstein et al. 2002*a*). Most of these studies aimed to measure how species respond to their habitat by removing spatial components in habitat variables (Keitt et al. 2002, Dale and Fortin 2002, Lichstein et al. 2002*a*,*b*). After addressing the issue of spatial autocorrelation in environmental variables, some studies still detect spatial aggregations in species distribution (Drolet et al. 1999, Lichstein et al. 2002*a*,*b*). When detected, such spatial aggregations are often treated as a statistical problem but can also be interesting in themselves (e.g., Dale and Fortin 2002). For example, spatial patterns at fine scales may be indicative of behavioral processes such as settlement preferences (Legendre 1993). As such, spatial aggregations of birds at fine scales deserve to be investigated as a potentially important biological phenomenon.

There could be important implications for conservation biology if a large number of forest bird species aggregate their territories independently of habitat features. Theoretically, species that aggregate their territories could show reduced population viability in highly fragmented landscapes, since remnant forest patches may remain unoccupied if they are too small to accommodate several territories (Smith and Peacock 1990, Ray et al. 1991, Lima and Zollner 1996). Thus, even though sizeable forest fragments may remain in a landscape, species that tend to aggregate may experience a greater loss of habitat than species with no tendency to aggregate. Moreover, after a local extinction, lack of conspecifics could impede recolonization of empty but otherwise suitable forest fragments if they remain unnoticed by settling individuals (Smith and Peacock 1990, Ray et al. 1991, Lima and Zollner 1996, Ward and Schlossberg 2004). These additive effects could result in the observed sensitivity to fragmentation reported for several species in the last 15 yr (review in Villard et al. 1999). Thus, knowing which species tend to aggregate could help identify species likely to be negatively affected by forest fragmentation. Species at risk could therefore be identified more readily (Fahrig and Merriam 1994, Wiens 1994).

Here, we report on the degree of aggregation of 17 forest bird species at various spatial scales, i.e., lags of 250-550 m, before and after controlling for the effects of vegetation structure. We also test whether spatially aggregated species respond more negatively to the amount of forest in the landscape. We addressed the latter prediction with species occurrence data obtained from the same study area.

METHODS

Study area

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

Avian surveys

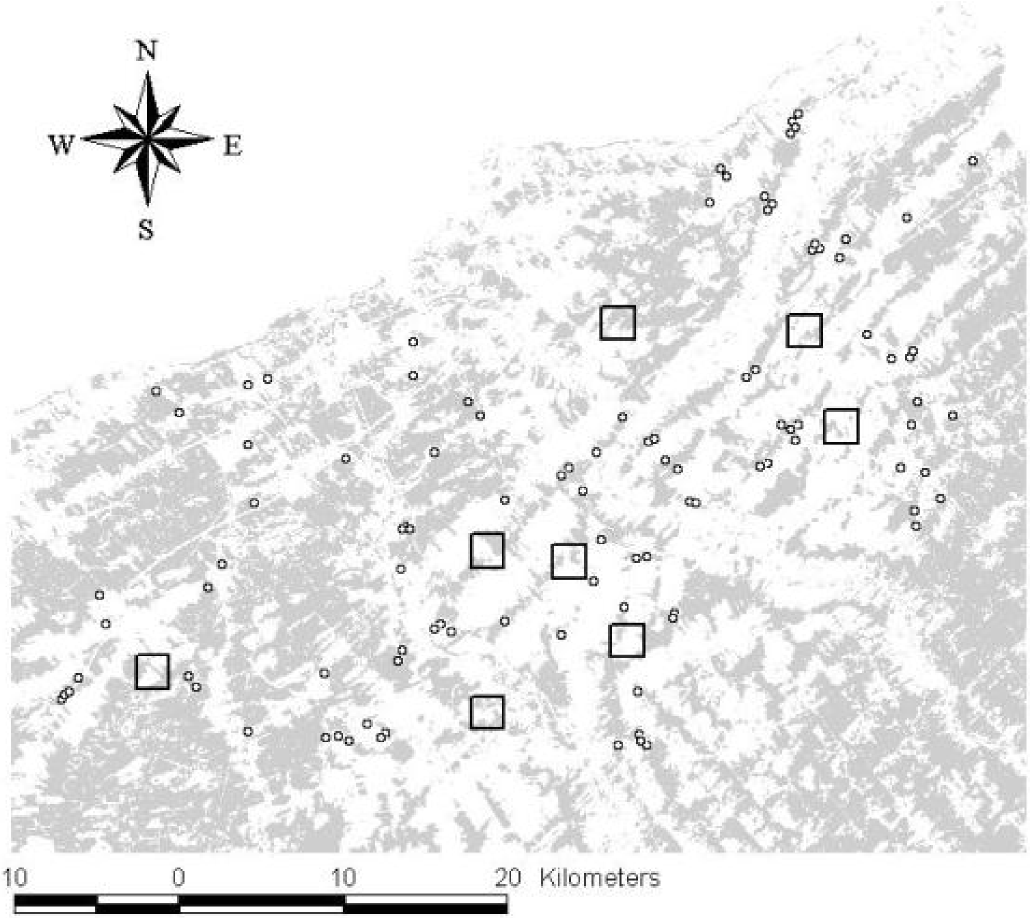
Within each plot, parallel transect lines were placed systematically on a north-south axis every 200 m. From 1 June to the first wk of July 2000 and 2001, each selected plot was surveyed once. Surveys took place in forested stands between 0500 and 1000 EST on days without wind or rain. During a typical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

Sampling stations were established systematically every 200 m along the transect lines for a total of 100 stations/plot. We kept only the sampling stations that were located within forested stands. Forested stands were defined as having ≥three trees within a 10 m radius. As a result, stations closer than 10 m from the edge of a wooded area were generally considered to be located in a forested stand. Among the eight plots, the number of stations within forested stands varied from 21 to 52 with a mean of 34 stations. After the surveys, each bird detection was assigned to the nearest sampling station. Thus, at each sampling station, we had information on the occurrence of each species.

Measuring spatial autocorrelation of bird occurrence

Only presence-absence data were used. We used Moran’s *I* coefficient (Legendre and Fortin 1989) to quantify the spatial autocorrelation for each species. Moran’s *I* varies between –1 and 1. For presence/absence data, negative values indicate distribution in regular arrays, e.g. caused by territorial spacing, whereas positive values indicate distribution in clusters, e.g. caused by conspecific attraction. For each species, we used the PASSAGE software (Rosenberg 2001) to analyze spatial autocorrelation using all sampling stations, i.e., within all woodland. We calculated spatial autocorrelation after accounting for the patchy nature of the forest. Thus, if a given species had been present at all stations, spatial autocorrelation would have been nonexistent, even though stations are clustered within forest patches. The degree of spatial autocorrelation of occurrence was measured at four spatial scales, i.e., lag distance: 250 m, 350 m, 450 m, and 550 m. The first lag distance interval (250 m) in the correlograms included all pairs of points separated by ≤250 m. Subsequent intervals contained all possible pairs of points separated by their respective lag distance. Intervals contained between 172 and 1055 pairs of points. Most songbird species defend territories ≤1 ha (Ehrlich et al. 1988). Furthermore, recent studies on the Least Flycatcher (*Empidonax minimus*) suggest that clusters may contain up to 30 individual territories (7.4 ± 1.4 territories, Tarof and Ratcliffe 2004). Thus, we assumed (1) that clusters of presence would occur at the chosen spatial scales, and (2) that our largest scale (550 m) would be sufficient to contain the largest aggregation for the species tested. For each species, four spatial autocorrelations were calculated, one for each lag distance. Therefore, significance of *I* was calculated with the progressive Bonferroni corrected α of 0.05/4 = 0.0125 (Legendre and Legendre 1998).

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



Accounting for local habitat variables

Between 31 May and 2 July 2000 and 2001, we delimited a 10-m radius circle around each sampling station. Within each circle, we recorded the occurrence of snags and sampled three vegetation strata: canopy (>7 m), subcanopy (2-7 m), shrubs (0.5-2 m), and ground (<0.5 m). Within each circle and for each stratum, we visually estimated the percent cover and height of each of the three most common species. Each station thus had a different set of species for each strata. These variables were chosen because we considered them to reflect structural differences among stations and to be important for forest songbird habitat. In previous studies, these variables have also been shown to accurately predict the occurrence of 162 bird species in Québec forests, i.e., between 83 and 93% of properly classified cases (DesGranges et al. 2001). We used principal component analysis to reduce the number of variables describing local habitat features with the SAS program, version 8 (SAS Institute Inc.

Table 1. Spatial autocorrelations of species occurrence as indicated by Moran’s *I* correlograms. Negative Moran’s *I* values indicate regular arrays, whereas positive values indicate clusters. Results of test: ** *P* <0.01, *** *P* <0.001.

Species	250 m	350 m	450 m	550 m
Yellow-bellied sapsucker *Sphyrapicus varius*	**0.16****	**0.12****	**0.07****	**0.07****
Eastern Wood-Pewee *Contopus virens*	0.06	0.08	0.06	0.05
Red-eyed vireo *Vireo olivaceaus*	**0.27*****	**0.27*****	**0.17*****	**0.17*****
Winter Wren *Troglodytes troglodytes*	0.22	0.06	-0.009	-0.008
Black-capped chickadee *Poecile atricapillus*	-0.07	**-0.11****	-0.03	-0.03
Veery *Catharus fuscescens*	0.10	0.06	0.06	0.06
Hermit thrush *Catharus guttatus*	**0.20*****	**0.20*****	**0.17*****	**0.17*****
American robin *Turdus migratorius*	<0.001	0.02	0.02	0.01
Nashville Warbler *Vermivora ruficapilla*	**0.41*****	**0.41*****	**0.31*****	**0.31*****
Chestnut-sided warbler *Dendroica pensylvanica*	**0.16****	**0.13*****	0.05	0.05
Magnolia warbler *Dendroica magnolia*	**0.26*****	**0.23*****	**0.24*****	**0.23*****
Black-throated blue warbler *Dendroica caerulescens*	0.09	0.09	0.02	0.02
Black-throated green warbler *Dendroica virens*	0.07	0.04	0.04	0.04

(con'd)

Blackburnian warbler *Dendroica fusca*	**0.16****	**0.12****	**0.10*****	**0.09*****
Black and white warbler *Mniotilta varia*	0.09	0.09	0.05	0.06
American redstart *Setophaga ruticilla*	**0.18*****	**0.14*****	**0.16*****	**0.16*****
Ovenbird *Seiurus aurocapilla*	**0.20*****	**0.16*****	**0.12*****	**0.12*****

1999). The first two components accounted for 43% of the variation present in the data. The first component mostly described an increase in ground cover height and in the percent cover of deciduous trees. The second component was associated with an increase in the percent cover of coniferous trees and in a decrease in the percent cover of deciduous trees.

We measured the spatial autocorrrelation of each of the first two components with Moran's *I* coefficient at four spatial scales, i.e., lag distance: 250 m, 350 m, 450 m, and 550 m. The spatial pattern of local habitat variables could thus be compared to the spatial pattern of occurrence of bird species. Similar patterns of autocorrelation between the two datasets would suggest that aggregative behavior in bird occurrence may simply reflect autocorrelated habitat variables within forest patches. Since the distribution of several species may reflect the availability of snags, we also measured the spatial autocorrelation of the occurrence of snags at 250 m, 350 m, 450 m, and 550 m.

We aimed to quantify spatial autocorrelation of avian occurrence while accounting for unwanted effects of vegetation structure. For each bird species, we conducted a general linear model with species occurrence as the dependent variable and the first two components as the independent variables. We then measured the spatial pattern of the Anscombe residuals from the general linear model. The degree of spatial autocorrelation of the residuals was measured at four spatial scales, i.e., lag distance: 250 m, 350 m, 450 m, and 550 m. Significance of Moran's *I* was calculated with the progressive Bonferroni corrected α of 0.05/4 = 0.0125 (Legendre and Legendre 1998).

Measuring avian landscape use

In a concurrent study, we surveyed 102 point count stations twice between 30 May and 29 June 2000 (Bourque 2005, Fig. 1). The point count stations were located outside of the eight plots mentioned above but in the same study area. The point count stations were spaced at least 250 m apart and were located >50 m from an edge. At each point count station, we recorded all individuals seen or heard within a 100 m radius. Each survey lasted 10 min and was conducted between 30 m before sunrise and 1000 EST, on mornings when weather was favorable. Additional details on bird point counts can be found in Bourque (2005).

LANDSAT-TM satellite images of the study area taken in 1993-1994 were classified into forest and non-forest habitats (Bélanger and Grenier 1998). We imported the satellite images into the ArcView 3.2 Geographic Information System (ESRI 1996). We used the Patch Analyst extension (Rempel 2000) to quantify landscape composition within circles centered on each point count station. Within each 500-m radius circle, we measured percent forest cover. Patch area or isolation was not used since forested areas were connected at the spatial scales we considered.

For each point count station, a species was considered present when it was detected in at least one of the two visits. For a given species, we measured the percent forest cover around the stations where this species occurred. The mean of this measure was used as an index of sensitivity to forest cover.

Association between spatial autocorrelation and landscape use

For 17 forest songbird species, we measured the degree of spatial autocorrelation of occurrence data at four spatial scales after removing unwanted effects of vegetation. For each species, the mean value of Moran's *I* was used as an index of spatial aggregation. Again for each species, sensitivity to forest cover was calculated by averaging the percent forest cover around each station where the species occurred. We predicted that species more sensitive to forest cover would also be more likely to be spatially autocorrelated. We used two types of analyses: correlations and the comparative phylogenetic analysis (Sanford et al. 2002). The latter analysis is performed when comparing closely related species, since they may share traits or adaptations through common ancestry. This situation creates a problem of dependence among species when using traditional correlation or regression analyses (Felseinstein 1985). However, the results were similar independent of the method that was used. We thus report hereafter only the results calculated with the correlations.

RESULTS

In analyses that ignored spatial components in habitat variables, nine out of 17 species significantly aggregated their territories in at least one spatial scale (Table 1). Additionally, the Black-capped Chickadee (*Poecile atricapillus*) showed negative autocorrelation, i.e., singing males tended to be located more evenly than by chance within woodland. Eight species aggregated their territories at all spatial scales (Table 1), whereas the location of an additional species was spatially aggregated in at least one spatial scale (Table 1). Spatial autocorrelations of vegetation attributes showed significant results only for the first component at 250 m (Table 2). Snags were present at 70% of sampling stations and were aggregated at all spatial scales measured (P <0.01).

Using residuals from general linear models did not alter results greatly (Table 3). Eight out of 17 species showed significant spatial aggregation in their occurrence data in at least one spatial scale (Table 3). After accounting for vegetation heterogeneity, there was no residual spatial aggregation of Yellow-bellied Sapsuckers (*Sphyrapicus varius*). Prior to removing the effects of local habitat variables, the Blackburnian Warbler (*Dendroica fusca*) and the Ovenbird (*Seiurus aurocapilla*) aggregated their territories at all spatial scales considered. After controlling for local habitat, these two species were spatially aggregated only at 450 m and 550 m.

The Winter Wren (*Troglodytes troglodytes*) and the Nashville Warbler (*Vermivora ruficapilla*) were the species most associated with forest cover (Table 4). The Chestnut-sided Warbler (*Dendroica pensylvanica*) and the American Redstart (*Setophaga ruticilla*) were the species least likely to occur in forested areas (Table 4). After controlling for local habitat, the relationship between spatial autocorrelation and landscape use was nearly significant (Pearson correlation coefficient = 0.47, P = 0.06; Fig. 2).

DISCUSSION

Our primary goal was to document spatial autocorrelation at small spatial scales for the greatest number of forest bird species. Nine species considered showed significant spatial aggregation on at least one spatial scale. Earlier studies have speculated that aggregative behavior may reflect autocorrelated habitat variables (Brown et al. 1995). We cannot rule out that the spatial aggregations of this study may reflect patterns of autocorrelations in local habitat variables that were not detected by our vegetation surveys. However, our results show that the observed aggregative patterns are likely a widespread occurrence in songbird populations, irrespective of the mechanisms behind this phenomenon. Also, we believe that our vegetation surveys accurately portrayed the habitat of our target species. Indeed, in a previous study (DesGranges et al. 2001), the habitat variables that we used accurately predicted avian assemblages in Québec forested ecosystems.

Of the 17 species studied, nine showed significant autocorrelations of their territories. Except for the Black-capped Chickadee, all autocorrelations were positive, a striking result in itself, given that

Table 2. Spatial autocorrelation of the first two components of a principal component analysis as indicated by Moran's *I* correlograms. Negative Moran's *I* values indicate regular arrays, whereas positive values indicate clusters. Numbers in bold are significant at P <0.001.

Spatial Scale (m)	First Principal Component	Second Principal Component
250	**0.145**	0.010
350	0.058	-0.005
450	0.013	-0.043
550	0.021	-0.037

territorial spacing is normally expected to yield regular arrays of singing males. In the case of the Black-capped Chickadee, territorial spacing likely occurs at a scale comparable to distance lags used. Indeed, chickadee territory size can reach 5 ha, whereas the territory size of the other species studied is generally ≤1 ha (Gauthier and Aubry 1996).

Other recent studies (Drolet et al. 1999, Lichstein et al. 2002*a*,*b*) have detected spatial aggregations in species occurrence and abundance even after controlling for the spatial pattern of habitat variables. For example, Lichstein et al. (2002*b*) found that the abundance of Black-throated Blue Warblers (*Dendroica caerulescens*) was significantly autocorrelated at 500-1000 m, i.e., lags of 150 m. In the same study, the abundance of the Chestnut-sided Warbler was not spatially autocorrelated at spatial scales ranging from 250-1000 m, whereas we found that Chestnut-sided Warbler males aggregated their territories. In another study, the abundances of the Eastern Wood-Pewee (*Contopus virens*) and of the Veery (*Catharus fuscescens*) were significantly autocorrelated within 1000 m (Lichstein 2002*a*). Furthermore, Drolet et al. (1999) found that the distribution of the Magnolia Warbler (*Dendroica magnolia*) was significantly autocorrelated within 1250 m. Most results from these other studies differ somewhat from ours. This may stem partly from differences in statistical analyses. There may also be geographic variation in the degree of spatial clustering of territories. Differences may also stem from the fact that we measured the clustering of occurrence data, whereas these other studies measured the clustering of abundance of their target species.

Species showed different levels of spatial autocorrelation before and after we controlled for habitat variables. For example, the occurrence of the Yellow-bellied Sapsucker was spatially autocorrelated at all spatial scales before controlling for habitat. However no spatial autocorrelation was found after controlling for the habitat of the Yellow-bellied Sapsucker. This suggests that the Yellow-bellied Sapsucker's distribution reflects local habitat variables, which may be spatially aggregated. Indeed, the aggregative pattern of the Yellow-bellied Sapsucker paralleled the pattern of snag clusters.

The distribution of two other species, the Blackburnian Warbler and the Ovenbird was significantly clustered before but not after controlling for habitat variables at 250 and 350 m. The first component of a principal component analysis of vegetation features was spatially aggregated only at 250 m. That first component represented mostly an increase in ground cover height and in the percent cover of deciduous trees.

Table 3. Moran's I correlograms of residuals from general linear models. Negative Moran's I values indicate regular arrays, whereas positive values indicate clusters. Results of test: ** $P < 0.01$, *** $P < 0.001$.

Species	250 m	350 m	450 m	550 m
Yellow-bellied sapsucker *Sphyrapicus varius*	0.06	<0.01	-0.02	-0.02
Eastern Wood-Pewee *Contopus virens*	-0.02	<0.01	-0.02	-0.02
Red-eyed vireo *Vireo olivaceaus*	**0.15****	**0.17*****	**0.09****	**0.09****
Winter Wren *Troglodytes troglodytes*	0.12	0.06	-0.01	-0.01
Black-capped chickadee *Poecile atricapillus*	-0.09	**-0.13****	-0.04	-0.04
Veery *Catharus fuscescens*	0.08	0.05	0.05	0.05
Hermit thrush *Catharus guttatus*	**0.15****	**0.16*****	**0.14*****	**0.14*****
American robin *Turdus migratorius*	0.01	0.02	0.02	0.02
Nashville Warbler *Vermivora ruficapilla*	**0.35*****	**0.35*****	**0.25*****	**0.25*****
Chestnut-sided warbler *Dendroica pensylvanica*	**0.16****	**0.13*****	0.05	0.05
Magnolia warbler *Dendroica magnolia*	**0.21*****	**0.18*****	**0.17*****	**0.16*****
Black-throated blue warbler *Dendroica caerulescens*	0.05	0.07	<0.01	<0.01
Black-throated green warbler *Dendroica virens*	0.08	0.04	0.05	0.05

(con'd)

Blackburnian warbler *Dendroica fusca*	0.12	0.09	**0.08****	**0.08****
Black and white warbler *Mniotilta varia*	0.07	0.09	0.06	0.06
American redstart *Setophaga ruticilla*	**0.15****	**0.11****	**0.13*****	**0.13*****
Ovenbird *Seiurus aurocapilla*	0.09	0.09	**0.08****	**0.08****

Therefore, the distribution of the Blackburnian Warbler and the Ovenbird likely reflects the clustered distribution of ground cover and/or percent cover of deciduous trees, at least at the 250 m scale.

After controlling for habitat variables, eight of the species that we studied showed no spatial autocorrelation: the Yellow-bellied Sapsucker, the Eastern Wood-Pewee, the Winter Wren, the Veery, the American Robin (*Turdus migratorius*), the Black-throated Blue Warbler, the Black-throated Green Warbler (*Dendroica virens*), and the Black-and-white Warbler (*Mniotilta varia*). The American Robin stands out among the species considered because it defends small territories, i.e., 0.1-0.3 ha (Young 1951, Eiserer 1976). The Yellow-bellied Sapsucker seemed to be associated with the aggregative patterns of snags, supporting findings from other studies (Kilham 1964, Tate 1973, Eberhardt 2000). The Winter Wren, the Veery, the Black-throated Blue Warbler, the Black-throated Green Warbler, and the Black-and-white Warbler are generally considered to be strongly associated with habitat features within their territories (Bertin 1977, Paszkowski 1984, Robbins et al. 1989, Holway 1991, Steele 1992, 1993, Kricher 1995, Robichaud and Villard 1999, Hejl et al. 2002). Such associations may have driven the occupancy pattern of these species. One other species, the Eastern Wood-Pewee is generally considered to be 'nearly ubiquitous' (McCarthy 1996) at both the local and landscape scale.

To our knowledge, our study is the first attempt to link spatial autocorrelation and landscape occupancy patterns. We found a strong tendency for species associated with forest cover to be spatially autocorrelated. However, one species, the Nashville Warbler may have had a disproportionate effect on the observed relationship. Adding more species would probably strengthen the relationship. In our study area, however, all available species were included in our analyses. Nevertheless, the results of our spatial autocorrelations may be relevant for the management of several of these species in fragmented landscapes. For example, three species significantly aggregated their territories at some spatial scales: the Chestnut-sided Warbler, the Blackburnian Warbler and the Ovenbird. The largest scale at which territorial clustering occurs in the Blackburnian Warbler and the Ovenbird has yet to be determined. But Chestnut-sided Warblers aggregate their territories at or below 350 m. Furthermore, five of the species considered (the Red-eyed Vireo [*Vireo olivaceus*], the Hermit Thrush [*Catharus guttatus*], the Nashville Warbler [*Vermivora ruficapilla*], the Magnolia Warbler, and the American Redstart [*Setophaga ruticilla*]) aggregated their territories at all spatial scales. This concurs with previous research that has found a negative impact of a decrease in forest cover on the distribution or fecundity of some of these species (Villard et al. 1993, Donovan et al. 1995, Robinson et al. 1995, Trzcinski et al. 1999, Bayne and Hobson 2001). For example, Ovenbirds are often associated to forest patches usually much larger than their territory (Van Horn and Donovan 1994, Ortega and Capen 1999, Porneluzi and Faaborg 1999, Bayne and Hobson 2002) and this could result from the need to aggregate (Lichstein et al. 2002*a,b*). Our results thus suggest that, in order to support

Table 4. Percent forest cover was calculated within 500-m radius circles centered on 102 point count stations. For each species, we present the mean percent forest cover around the stations where this species occurred. Data were collected in 2000 within 50 km of Quebec City (46°45’ N, 71°20’ W), Québec, Canada.

Species	Mean percent forest cover
Yellow-bellied sapsucker *Sphyrapicus varius*	53.9
Eastern Wood-Pewee *Contopus virens*	49.9
Red-eyed vireo *Vireo olivaceaus*	50.4
Winter Wren *Troglodytes troglodytes*	58.6
Black-capped chickadee *Poecile atricapillus*	50.1
Veery *Catharus fuscescens*	52.0
Hermit thrush *Catharus guttatus*	56.4
American robin *Turdus migratorius*	53.1
Nashville Warbler *Vermivora ruficapilla*	63.1
Chestnut-sided warbler *Dendroica pensylvanica*	45.2
Magnolia warbler *Dendroica magnolia*	56.5
Black-throated blue warbler *Dendroica caerulescens*	52.1
Black-throated green warbler *Dendroica virens*	53.3

(con'd)

Blackburnian warbler *Dendroica fusca*	51.9
Black and white warbler *Mniotilta varia*	54.3
American redstart *Setophaga ruticilla*	46.5
Ovenbird *Seiurus aurocapilla*	52.5

whatever processes are served by aggregative behavior and associated fitness benefits (Doligez et al. 2004*a*) these species need large or connected portions of suitable habitat. Furthermore, future research should try to determine if these species exhibit territorial aggregations at spatial scales larger than 550 m. Results from such studies would help refine management recommendations for these species.

Responses to this article can be read online at:
http://www.ace-eco.org/vol1/iss2/art3/responses/

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LITERATURE CITED

Alatalo, R. V., A. Lundberg, and M. Björklund. 1982. Can the song of male birds attract other males? An experiment with the pied flycatcher *Ficedula hypoleuca*. *Bird Behavior* **4**:42-45.

Bayne, E. M., and K. A. Hobson. 2002. Apparent survival of male Ovenbirds in fragmented and forested boreal landscapes. *Ecology* **83**:1307-1316.

Bayne, E. M., and K. A. Hobson. 2001. Effects of habitat fragmentation on pairing success of Ovenbirds: importance of male age and floater behavior. *Auk* **118**:380-388.

Bélanger, L., and M. Grenier. 1998. *Importance et causes de la fragmentation forestière dans les agroécosystèmes du sud du Québec*. Direction de la conservation de l'environnement, Service canadien de la faune, région du Québec, Environnement Canada, Sainte-Foy, Québec, Canada.

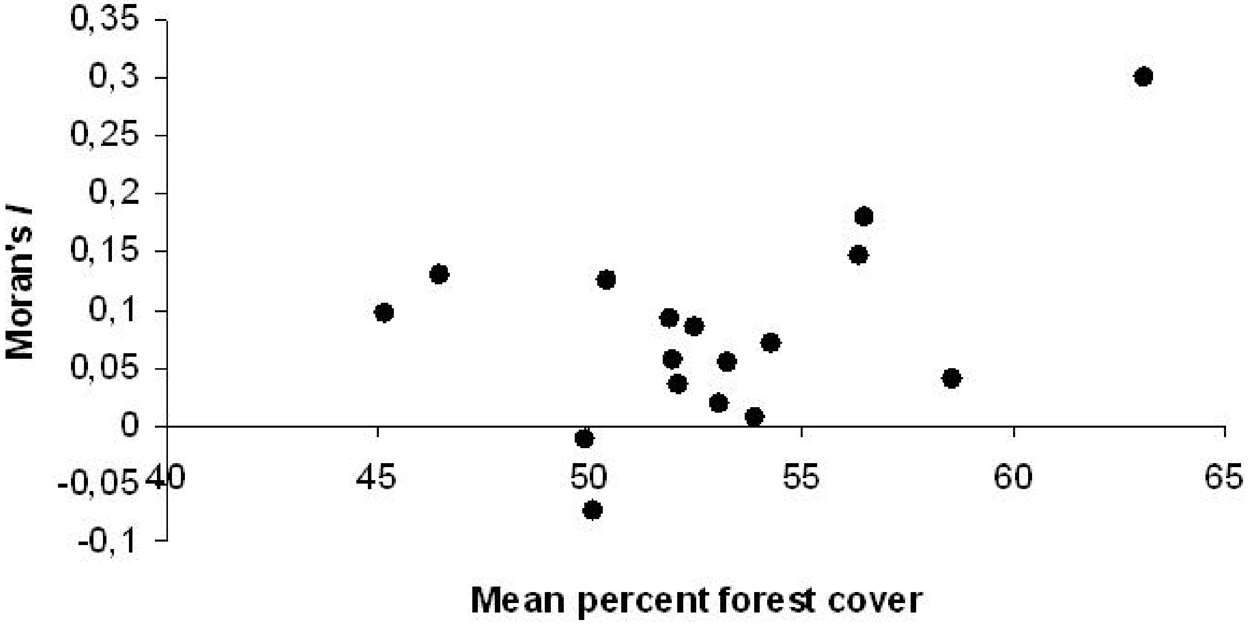
Bertin, R. I. 1977. Breeding habitats of the Wood Thrush and Veery. *Condor* **79**:303-311.

Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. *Bird census techniques*. Academic Press, San Diego, California, USA.

Bildstein, K. L. 1983. Why white-tailed deer flag their tails. *American Naturalist* **121**:709-715.

Bourque, J. 2005. *Déterminants comportementaux de la répartition spatiale des oiseaux dans les forêts fragmentées*. Dissertation, Université Laval,

Fig. 2. Sensitivity to forest cover and spatial autocorrelation of residuals, calculated with Moran’s *I* coefficient, for 17 forest bird species, within 50 km of Quebec City (46°45’ N, 71°20’ W), Québec, Canada. Each dot represents a species.



Québec, Québec, Canada.

Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. *Ecology* **76**:2028-2043.

Dale, M. R. T., and M.-J. Fortin. 2002. Spatial autocorrelation and statistical tests in ecology. *Écoscience* **9**:162-167.

DesGranges, J.-L., P. Agin, and S. Bengio. 2001. The use of predictive models of breeding bird assemblages for assessing and monitoring forest bird diversity. Pages 181-200 *in* A. Franc, O. Laroussinie, and T. Karjalainen, editors. *Criteria and indicators for sustainable forest management at the forest management unit level*. European Forest Institute Proceedings, Number 38, Nancy, France.

Doligez, B., E. Danchin, J. Clobert, and L. Gustafsson. 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *Journal of Animal Ecology* **68**:1193-1206.

Doligez, B., T. Pärt, E. Danchin, J. Clobert, and L. Gustafsson. 2004*a*. Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. *Journal of Animal Ecology* **73**:75-87.

Doligez, B., T. Pärt, and E. Danchin. 2004*b*. Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection? *Animal Behaviour* **67**:457-466.

Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* **9**:1380-1395.

Drolet, B., A. Desrochers, and M.-J. Fortin. 1999. Effects of landscape structure on nesting songbird distribution in a harvested boreal forest. *Condor* **101**:699-704.

Eberhardt, L. S. 2000. Use and selection of sap trees by Yellow-bellied Sapsuckers. *Auk* **117**:41-51.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. *The birder's handbook: a field guide to the natural history of North American birds.* Simon and Schuster/Fireside, New York, New York, USA.

Eiserer, L. A. 1976. *The American Robin.* Nelson-Hall, Chicago, Illinois, USA.

ESRI. 1996. *ArcView® 3.2 GIS.* Environmental Systems Research Institute Inc., Redlands, California, USA.

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* **8**:50-59.

Felseinstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* **125**:1-15.

Gauthier, J., and Y. Aubry. 1996. *The breeding birds of Québec: atlas of the breeding birds of southern Québec.* Association Québécoise des Groupes d'Ornithologues, Province of Québec Society for the Protection of Birds, Canadian Wildlife Service, Environnement Canada (Québec region), Montréal, Québec, Canada.

Hagan, J. M., P. S. McKinley, A. L. Meehan, and S. L. Grove. 1997. Diversity and abundance of landbirds in a northeastern industrial forest. *Journal of Wildlife Management* **61**:718-735.

Hejl, S. J., J. A. Holmes, and D. E. Kroodsma. 2002. Winter Wren (*Troglodytes troglodytes*). *In* A. Poole and F. Gill, editors. *Birds of North America,* Number 623. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

Holway, D. A. 1991. Nest-site selection and the importance of nest concealment in the black-throated blue warbler. *Condor* **93**:575-581.

Keitt, T. H., O. N. Bjørnstad, P. H. Dixon, and S. Citron-Pousty. 2002. Accounting for spatial pattern when modeling organism-environment interactions. *Ecography* **25**:616-625.

Kenward, R. E. 1978. Hawks and doves: attack success and selection in goshawk flights at wood-pigeons. *Journal of Animal Ecology* **47**:449-460.

Kiester, A. R., and M. Slatkin. 1974. A strategy of movement and resource utilization. *Theoretical Population Biology* **6**:1-20.

Kilham, L. 1964. The relations of breeding Yellow-bellied Sapsuckers to wounded birches and other trees. *Auk* **81**:520-527.

Koenig, W. D. 1998. Spatial autocorrelation in California land birds. *Conservation Biology* **12**:612-620.

Koenig, W. D. 2001. Spatial autocorrelation and local disappearances in wintering North American birds. *Ecology* **82**:2636-2644.

Kricher, J. C. 1995. Black-and-white Warbler (*Mniotilta varia*). *In* A. Poole and F. Gill, editors. *Birds of North America,* Number 158. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* **74**:1659-1673.

Legendre, P. and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* **80**:107-138.

Legendre, P., and L. Legendre. 1998. *Numerical ecology.* Second English edition. Elsevier Science, Amsterdam, The Netherlands.

Lichstein, J. W., T. R. Simons, and K. E. Franzreb. 2002*a*. Landscape effects on breeding songbird abundance in managed forests. *Ecological Applications* **12**:836-857.

Lichstein, J. W., T. R. Simons, S. A. Shriner, and K. E. Franzreb. 2002*b*. Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs* **72**:445-463.

Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* **11**:131-135.

McCarty, J. P. 1996. Eastern Wood-Pewee (*Contopus virens*). *In* A. Poole and F. Gill, editors. *Birds of North America*, Number 245. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

McGarigal, K., and W. C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecological Monographs* **65**:235-260.

Mennill, D. J., S. M. Ramsay, P. T. Boag, and L, M. Ratcliffe. 2004. Patterns of extrapair mating in relation to male dominance status and female nest placement in black-capped chickadees. *Behavioral Ecology* **15**:757-765.

Muller, K. L., J. A. Stamps, V. V. Krishnan, and N. H. Willits. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). *American Naturalist* **150**:650-661.

Norris, D. R., and B. J. M. Stutchbury. 2001. Extraterritorial movements of a forest songbird in a fragmented landscape. *Conservation Biology* **15**:729-736.

Ortega, Y. K., and D. E. Capen. 1999. Effects of forest roads on habitat quality for Ovenbirds in a forested landscape. *Auk* **116**:937-946.

Pärt, T., and B. Doligez. 2003. Gathering public information for habitat selection: prospecting birds cue on parental activity. *Proceedings of the Royal Society of London Series B, Biological Sciences* **270**:1809-1813.

Paszkowski, C. A. 1984. Macrohabitat use, microhabitat use, and foraging behavior of the Hermit Thrush and Veery in a northern Wisconsin forest. *Wilson Bulletin* **96**:286-292.

Penhollow, M. E., and D. F. Stauffer. 2000. Large scale habitat relationships of Neotropical migratory birds in Virginia. *Journal of Wildlife Management* **64**:362-373.

Perry, E. F., and D. E. Andersen. 2003. Advantages of clustered nesting for least flycatchers in north-central Minnesota. *Condor* **105**:756-770.

Porneluzi, P. A., and J. Faaborg. 1999. Season-long fecundity, survival, and viability of Ovenbirds in fragmented and unfragmented landscapes. *Conservation Biology* **13**:1151-1161.

Ray, C., M. Gilpin, and A. T. Smith. 1991. The effect of conspecific attraction on metapopulation dynamics. *Biological Journal of the Linnean Society* **42**:123-134.

Reed, J. M., and A. P. Dobson. 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology and Evolution* **8**:253-256.

Rempel, R. 2000. *Patch Analyst 2.2.* Center for Northern Forest Ecosystem Research, Lakehead University Campus, Thunder Bay, Ontario, Canada.

Robbins, C. R., D. K. Dawson and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildlife Monographs* **103**:1-34.

Robichaud, I., and M.-A. Villard. 1999. Do Black-throated Green Warblers prefer conifers? Meso- and microhabitat use in a mixedwood forest. *Condor* **101**:262-271.

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.

Rosenberg, M. S. 2001. *Passage. Pattern analysis, spatial statistics, and geographic exegesis.* Version 1.1. Department of Biology, Arizona State University, Tempe, Arizona, USA.

Sanford, G. M., W. I. Lutterschmidt, and V. H. Hutchison. 2002. The comparative method revisited. *Bioscience* **52**:830-836.

SAS Institute Inc. 1999. *SAS Release.* Version 8.00. SAS Institute Inc., Cary, North Carolina, USA.

Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology* **78**:1914-1932.

Smith, A. T., and M. M. Peacock. 1990. Conspecific attraction and the determination of metapopulation colonization rates. *Conservation Biology* **4**:320-323.

Stamps, J. A. 1987. Conspecifics as cues to territory quality: a preference for previously used territories by juvenile lizards (*Anolis aeneus*). *American Naturalist* **129**:629-642.

Stamps, J. A. 1988. Conspecific attraction and territorial aggregation: a field experiment. *American Naturalist* **131**:329-347.

Stamps, J. A. 1994. Territorial behavior: testing the assumptions. *Advances in the Study of Behavior* **23**:173-232.

Stamps, J. A. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. Pages 230-242 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. *Dispersal*. Oxford University Press Inc., New York, New York, USA.

Steele, B. B. 1992. Habitat selection by breeding Black-throated Blue Warblers (*Dendroica caerulescens*) at two spatial scales. *Ornis Scandinavia* **23**:33-42.

Steele, B. B. 1993. Selection of foraging and nesting sites by Black-throated Blue Warblers: their relative influence on habitat choice. *Condor* **95**:568-579.

Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution* **14**:401-405.

Tarof, S. A., and L. M. Ratcliffe. 2004. Habitat characteristics and nest predation do not explain clustered breeding in least flycatchers (*Empidonax minimus*). *Auk* **121**:877-893.

Tarof, S. A., L. M. Ratcliffe, M. M. Kasumovik, and P. T. Boag. 2005. Are least flycatcher (*Empidonax minimus*) clusters hidden leks? *Behavioral Ecology* **16**:207-217.

Tate, J., Jr. 1973. Methods and annual sequence of foraging by the sapsucker. *Auk* **90**:840-856.

Trzcinski, K. M., L. Fahrig, and G. Merriam. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications* **9**:586-593.

Van Horn, M. A., and T. M. Donovan. 1994. Ovenbird (*Seiurus aurocapillus*). *In* A. Poole and F. Gill, editors. *Birds of North America* Number 88. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

Villard, M.-A., P. R. Martin, and C. G. Drummond. 1993. Habitat fragmentation and 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.

Wagner, R. H. 1997. Hidden leks: sexual selection and the clustering of avian territories. Pages 123-145 *in* P. G. Parker and N. Burley, editors. *Avian reproduction*. Ornithological Monographs, number 49. Oxford University Press, Oxford, UK.

Ward, M. P., and S. Schlossberg. 2004. Conspecific attraction and the conservation of territorial songbirds. *Conservation Biology* **18**:519-525.

Wiens, J. A. 1994. Habitat fragmentation: island vs. landscape perspectives on bird conservation. *Ibis* **137**:S97-S104.

Young, H. 1951. Territorial behavior of the Eastern Robin. Proceedings. *Linnean Society of New York* **58-62**:1-37.