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White-throated Sparrow Response to Forest Harvesting in North-Central Alberta: Results Not So Clear-Cut?

Réaction du Bruant à gorge blanche à l'exploitation forestière dans le centre-nord de l'Alberta

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ABSTRACT. The use of density to measure a species' responses to habitat change remains prevalent despite warnings that relying on such parameters can be misleading. We evaluated whether density was a useful surrogate of habitat quality for the White-throated Sparrow (*Zonotrichia albicollis*), an apparent habitat generalist, in a recently logged landscape near Calling Lake, Alberta, Canada. We detected significant differences in the territory density of birds among three distinct habitat types: interior forest, forest edges, and recent (4- to 6-yr-old) clear-cuts. However, the observed patterns in territory density were not consistent with several indices of habitat quality. We found a consistent and marked gradient for indices such as nesting success (based on a reproductive index), pairing success, and the proportion of territories that successfully fledged young between interior forest sites and clear-cuts. Edge habitats, in which high relative density offset lower reproductive success, represented moderate-quality habitat for this species. Our results suggest that the continued use of density alone, without some measure of habitat quality, is insufficient if not misleading when evaluating response to habitat change. Our results have important implications for understanding the population dynamics of this species, which is often overlooked in population-level studies yet continues to experience long-term population declines over large portions of its breeding range.

RÉSUMÉ. L'utilisation de la densité afin de mesurer la réaction d'une espèce à la suite d'un changement dans son habitat demeure prédominante, en dépit des avertissements quant au risque d'erreur relié à l'utilisation de ce genre de paramètres. Nous avons évalué la valeur de la densité en tant qu'indicateur de la qualité de l'habitat pour le Bruant à gorge blanche (*Zonotrichia albicollis*), une espèce apparemment généraliste du point de vue de l'habitat, dans un paysage ayant récemment subi une coupe forestière, près du lac Calling en Alberta, au Canada. Nous avons détecté des différences significatives entre les densités territoriales des oiseaux dans trois types d'habitats distincts : l'intérieur de la forêt, les bordures de la forêt et les coupes à blanc récentes (datant de 4 à 6 ans). Toutefois, les patrons observés pour les densités territoriales ne correspondaient pas aux patrons révélés par plusieurs indices de la qualité de l'habitat. Nous avons trouvé un gradient constant et marqué pour des indices comme le succès de nidification (basé sur un indice de reproduction), le succès d'appariement et la proportion de territoires où des jeunes ont pris leur envol avec succès entre les sites à l'intérieur de la forêt et les coupes à blanc. Les habitats de bordure, où la densité relative élevée compense pour le succès de reproduction plus faible, représentaient des habitats de qualité moyenne pour cette espèce. Nos résultats laissent croire que l'utilisation de la seule densité, sans autre mesure de la qualité de l'habitat, est insuffisante sinon trompeuse pour évaluer la réponse à un changement de l'habitat. Nos résultats ont d'importantes implications dans la compréhension de la dynamique de la population de l'espèce, laquelle est souvent négligée dans les études à l'échelle des

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populations, mais qui continue pourtant de subir un déclin à long terme dans de grandes portions de son aire de reproduction.

INTRODUCTION

Concern over declines in many species of North American songbirds has prompted extensive research into potential causes. However, gathering detailed information for numerous species over large areas and within limited sampling periods remains challenging (Vickery et al. 1992, Ralph et al. 1995). Consequently, most research relies on time-efficient, broad-scale survey techniques (Ralph et al. 1995), often amounting to breeding season counts of territorial singing males (Dejong and Emlen 1985, McShea and Rappole 1997). Although surveys of this type are efficient, their results may be misleading because the mere presence, abundance, or density of a species in a particular habitat may not be indicative of the quality of that habitat (Van Horne 1983, Vickery et al. 1992, Rangen et al. 2000). Further, the disconnect between density and habitat quality as measured by the habitat-specific performance or condition of birds (Johnson 2007) may be greatest in human-modified habitats if birds are unable to properly evaluate habitat quality (Misenhelter and Rotenberry 2000, Pidgeon et al. 2003). Although human-modified habitats may provide equivalent or even superior resources for some species, for many others these habitats represent ecological traps. Although human-modified habitats may appear suitable, individuals settling in these habitats may experience lower reproductive success compared to individuals occupying more natural habitats (Gates and Gysel 1978, Purcell and Verner 1998, Remes 2003). This disconnect may also be more pronounced in locations in which large-scale human disturbance is relatively recent and individuals may not distinguish ecological traps from ecological opportunities (Misenhelter and Rotenberry 2000, Pidgeon et al. 2003, Bock and Jones 2004).

Recent but rapidly increasing anthropogenic disturbance in western Canada, particularly in Alberta, has fragmented the southern boreal forest and led to considerable habitat loss and alteration (Schneider et al. 2003, Bayne et al. 2005). Despite the fact that bird distribution and abundance data suggest that the boreal plains of western North America are extremely important to landbirds, there remains a paucity of information on the basic ecology and habitat requirements of most songbirds breeding in this region (Schmiegelow et al. 1997, Machtans and Latour 2003). Habitat specialists have received some research attention because they are thought to be the most sensitive to habitat disturbance (Robichaud and Villard 1999, Bayne and Hobson 2001, Warkentin et al. 2003). However, habitat quality for generalist species could be incorrectly evaluated when relying solely on density comparisons, because individuals may continue to occupy human-disturbed habitats despite experiencing lower reproductive success (Fort and Otter 2004).

The White-throated Sparrow (*Zonotrichia albicollis*) is one of the most abundant songbirds breeding in the boreal forest of North America, with close to 80% of the global range of this species occurring within this biome (Blancher 2003). Given its seemingly ubiquitous distribution in different habitat types, the species has been described not only as a habitat generalist (Falls and Kopachena 1994, Rail et al. 1997, Drapeau et al. 2000, Schieck and Song 2006), but also as an edge species (Freemark and Merriam 1986, Freemark and Collins 1996, Jobes et al. 2004) and an early-successional species (Crete et al. 1995, Imbeau et al. 1999). White-throated Sparrows are also known to establish territories and breed in recent clear-cuts (Darveau et al. 1997, Schmiegelow et al. 1997, Machtans and Latour 2003). In spite of this apparent ubiquity, White-throated Sparrows have exhibited rangewide declines of 0.6 %/yr in recent decades based on Breeding Bird Survey (BBS) data (Sauer et al. 2007). The White-throated Sparrow has also been identified as a conservation priority among Canadian landbirds based on observed population declines and stewardship responsibility (Dunn et al. 1999). According to BBS data, populations in the

eastern portion of the species' range have experienced the most persistent declines (Sauer et al. 2007), perhaps given the longer history of land disturbance and habitat loss (Bock and Jones 2004, Schrott et al. 2005) and the limited tolerance or resilience of eastern conspecifics to anthropogenic disturbance (Bélisle et al. 2007). Although the BBS did not document declines in the western portion of the species' range (Sauer et al. 2007), evaluation of response to habitat alteration and fragmentation has consisted largely of assessments of abundance or density, without any substantive evaluations of habitat quality (Schmiegelow et al. 1997).

To explore the relationship between density and habitat quality for the White-throated Sparrow, we compared territory density in three habitat types to several habitat quality indices. Specifically, we compared density to male territory settlement patterns, male body condition, nesting success using actual nests and a reproductive index method, fledging success, i.e., the number of independent offspring produced, and site fidelity in interior forest, forest edges, and recent clear-cuts in a western boreal forest landscape. Our goals were to determine whether density was a useful indicator of habitat quality in this seemingly generalist species and to better understand potential resilience to longer-term forest harvesting in this region.

METHODS

Study area

Our study was conducted in a deciduous-dominated mixedwood boreal forest near Calling Lake, Alberta, Canada (55°15'N, 113°19'W), between 1998 and 2000 as part of the Calling Lake Fragmentation Experiment (see Schmiegelow et al. 1997). The study area was harvested in the winter of 1993–1994 as part of a larger investigation of songbird community dynamics before and after experimental forest fragmentation (see Schmiegelow et al. 1997). Our study design consisted of three 10-ha (250 x 400 m) sites located in three broad habitat types, i.e., interior forest, forest edges, and recent clear-cuts, each replicated three times (Fig. 1). Interior forest sites were mixed stands of old (120- to 140-yr) deciduous-dominated forest with an overstory composed of trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), and white birch (*Betula papyrifera*). Interior forest sites were

located a minimum of 200 m from a forest/clear-cut edge. Edge sites, consisting of pairs of 125 x 250 m subplots, were located in mixed stands of old forest adjacent to clear-cuts and extended from the forest/clear-cut edge to 125 m into the forest. Our edge definition was largely defined by our sampling methodology rather than an a priori assumption about potential edge effects. Clear-cut sites were located in 250-m-wide, 4- to 6-yr-old regenerating forest in harvested areas formerly consisting of old mixed forest. The clear-cuts did not receive any postharvest site treatment and contained 1–2.5 m regenerating aspen, poplar, and birch. Clear-cut and edge sites were located adjacent to each other; replicates of all treatment sites were a minimum of 250 m apart.

Bird territory density

We used spot-mapping (Robbins 1970) to determine White-throated Sparrow density, conducting 12 surveys from 16 May to 23 July 1998 and 16 surveys from 2 May to 25 July 1999. We surveyed each site every 2–7 d during the breeding season, increasing the frequency of surveys during egg laying and incubation when birds were more detectable (Gibbs and Wenny 1993) and reproductive behaviours might be more easily observed. To reduce potential sampling bias, we alternated observers and start locations at each site on each survey. In both years, surveys were conducted by a total of three observers, two of whom were present in both years. Each survey was conducted between 0500 and 1000 h during the peak hours of male territorial singing (Bibby et al. 1997). A survey was halted during high winds or in the event of measurable precipitation, and the area was resurveyed on the next fair-weather day. A male bird was considered territorial if it was detected singing in the same area for ≥ 10 days, was paired, or showed any evidence of nesting (Robbins 1970). To improve our ability to distinguish territorial individuals, we captured White-throated Sparrows in mist nets using playbacks of recorded song. Each bird was given a unique combination of two (1998) or three (1999) colored plastic leg bands and one U.S. Fish and Wildlife Service aluminum band. Only those territories with > 50% of mapped locations (minimum three points) occurring within the boundaries of a site were included in analyses. Territories that straddled the clear-cut/edge interface were assigned to the treatment within which > 50% of the detections occurred. We used

Fig. 1. Schematic diagram of study layout showing forested areas (white) and regenerating clear-cuts (dotted) from Calling Lake, Alberta. Interior forest sites are in black, with edge sites in gray and clear-cut sites indicated by hatched lines.
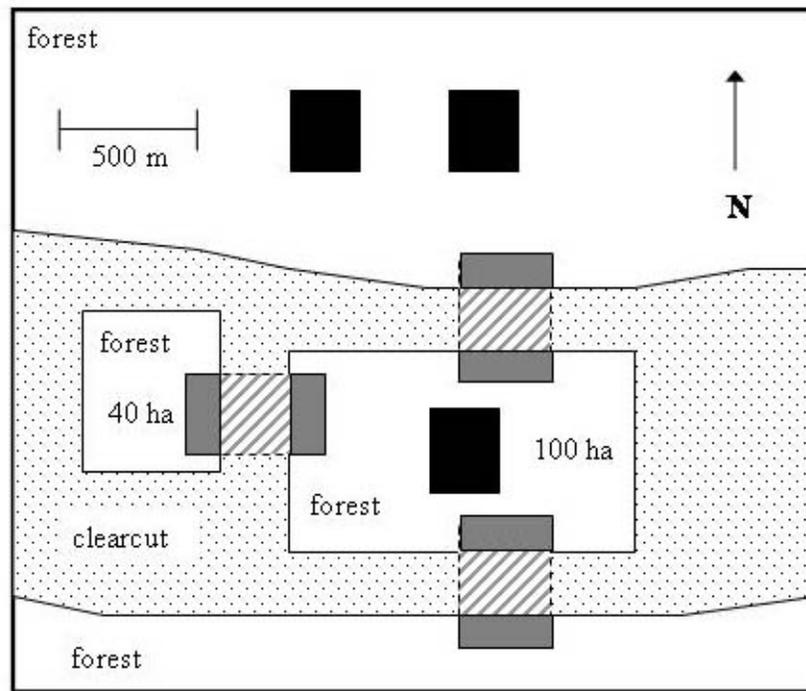
the number of territorial males per site as our measure of density.

Settlement patterns

We monitored the settlement patterns of male White-throated Sparrows arriving on the breeding grounds using spot-mapping. Settlement pattern is defined as the mean date of territory occupancy for all individuals within a specific habitat type. Only singing males that occupied a relatively small area, i.e., 1 ha or roughly the size of an average breeding territory, for a minimum of 10 d were considered territorial and were included in the analysis. Surveys were initiated too late in the spring of 1998 to properly document the arrival of territorial birds, so settlement patterns were compared using data collected in May 1999 and May 2000.

Many territorial birds abandoned breeding territories occupied for ≥10 d, suggesting that these sites may have been suboptimal for nesting. Thus, we compared rates of territory abandonment among habitat types to determine whether abandonment was an indicator of habitat quality.

Body condition

We captured White-throated Sparrows in mist nets using song playback. For each captured bird, we determined sex through a combination of wing length and the presence of cloacal protuberance (Pyle et al. 1997); however, we were unable to reliably determine the age of captured birds. We measured wing length to the nearest millimeter using unflattened wing chord, and body mass to the nearest gram using a 50-g Pesola spring balance. Body condition was estimated using the ratio of

body mass to wing chord length (Winker et al. 1992). Given the low sample size of captured females and the variability in body mass imposed by the physiological demands on females during the breeding season, females were not included in comparisons of body condition.

Reproductive success

We measured nesting success in 1998 and 1999 both directly, by locating and monitoring active White-throated Sparrow nests, and indirectly through the use of a reproductive index (Vickery et al. 1992, Dale et al. 1997, Rangen et al. 2000, Harris and Reed 2002). Mapped territories were ranked on a scale from 1 to 5 on the basis of behavioral cues, with increasing evidence of nesting success (see Vickery et al. 1992; Table 1). Birds in this population generally produced a single brood each year, although we discontinued our surveys when the majority of territories had fledged their first brood of offspring to avoid confusion with possible second broods. Given the difficulty of observing certain reproductive behaviors, such as adults carrying nesting material or food (ranks 3 and 4, respectively, in Table 1), the resulting bimodal distribution of reproductive index values may be a limitation of this technique (Fig. 2). Because we were ultimately interested in knowing whether a given territory was reproductively successful, we collapsed our reproductive index values and treated reproductive success as a binary variable in which ranks 1–4 were considered not successful (0) and rank 5 was considered successful (1). Hereafter, unless otherwise specified, nesting success refers to the proportion of territories that successfully fledged young, as derived from our reproductive index. We also used the reproductive index method to estimate rates of pairing success. Male territories with a rank of 1 were considered unpaired and those with ranks of ≥ 2 were considered to be successfully paired.

We compared the productivity of monitored territories among habitat types by taking the largest single count of fledglings in the presence of adults during the breeding season. We banded a large proportion of territorial adult birds and nestling birds in both years, thereby improving our ability to determine fledgling origin and minimizing the potential for overestimating the number of fledglings produced by a single pair. Young birds often remain in their natal territories following their parents for up to 2 weeks after fledging (Falls and Kopachena 1994). Adults are very sensitive to

disturbance during this stage, and when human observers approach young, birds respond with alarm calls and distraction displays (Falls and Kopachena 1994), thereby increasing the probability of detecting family groups.

Site fidelity

To compare male site fidelity among habitat types, color-marked individuals were relocated in subsequent years using spot-mapping (Robbins 1970). In 1999, 16 spot-mapping surveys were conducted throughout the breeding season, and in 2000 10 surveys were conducted during the month of May. Only individuals that returned to the same 10-ha study site they had occupied at the end of previous year's breeding season were included in estimates of site fidelity.

Statistical analyses

We used a mixed-effects modeling approach (Pinheiro and Bates 2000) to examine the relationship between habitat type, i.e., clear-cut, edge, and forest interior, and measures of White-throated Sparrow density, body condition, nesting success, and site fidelity. This approach allowed us to account for the fixed effect of habitat type as well as the repeated measurement of the same plots in two years by using plot as a random effect in our models. To fit models with continuous response variables such as territory density (males/10 ha), male body condition (weight divided by wing chord), and fledgling success (fledglings/10 ha), we used linear mixed-effects models with maximum likelihood parameter estimation ("lme," package nlme). To fit models with binomial response variables, e.g., male return to breeding site = 1/0, nesting success = 1/0, and pairing success = 1/0, as the response variables, we used generalized linear mixed models with the penalized quasi-likelihood method of parameter estimation ("glmmPQL," library MASS) using R version 2.6.1 (R Development Core Team 2007). In all models, habitat type was a fixed effect and plot was a random effect.

Independent samples t tests were used to compare mean territory density and mean male mass between 1998 and 1999, Mann-Whitney U tests were used to compare mean male wing chord between years, and chi-square tests were used to compare nest success and site fidelity between years. Spearman's

Table 1. Reproductive index rankings for a single-brooded species. These values represent the most advanced stage of nesting observed on the territory.

Rank	Definition
1	Territorial male present 4+ weeks
2	Territorial male and female present 4+ weeks
3	Pair found nest building, laying or incubating eggs, or giving distraction display
4	Adults carrying food to presumed nestlings
5	Evidence of fledging success

rank correlations were used to test for relationships between male body mass and time of day or Julian date. Kruskal-Wallis tests were used to compare average settlement date among habitat types.

In all analyses, we considered $P \leq 0.05$ to be highly significant and $0.05 > P \leq 0.10$ to be marginally significant. All data are presented as mean $\pm$ SE, unless otherwise stated.

RESULTS

Bird territory density

For the White-throated Sparrow in this study, average territory density did not differ significantly between years (independent samples t test: $t_{16} = 0.48$, $P = 0.64$), with a mean density of 11.8 ± 1.18 per site ($n = 106$ territories) in 1998 and 10.9 ± 1.43 per site ($n = 98$ territories) in 1999. Territory density was highest in edge habitat in both years, and lowest in clear-cuts (Fig. 3). Habitat type was a significant predictor of variation in territory density (Table 2).

Settlement patterns

Overall, differences in dates of settlement of male White-throated Sparrows on territories were not significant among habitat types (Kruskall-Wallis test: $\chi^2 = 0.20$, $n = 192$, $P = 0.90$). For both years combined, the average date of territory settlement was slightly earlier in edge and interior forest sites (13 May) than in clear-cut sites (16 May).

Birds that were not reproductively successful appeared to abandon territories in clear-cut sites at higher rates than in edge or interior forest sites. Fewer territories were abandoned throughout the breeding season in interior forest (2/37 or 5%) and edge sites (10/58 or 17%) than in clear-cuts (25/38 or 66%).

Body condition

A total of 92 male White-throated Sparrows were banded in 1998 ($n = 51$) and 1999 ($n = 41$). Males were captured, weighed, and measured between May 6 and July 16 1998 (05:40–16:30 h) and between May 7 and June 12 1999 (05:45–15:10 h). Mean male mass was significantly higher in 1998 (26.8 ± 0.20 g) than in 1999 (25.5 ± 0.20 g; $t_{90} = 4.45$, $P < 0.001$). Male wing chord did not differ significantly between years, with a mean of 73.6 ± 0.28 mm in 1998 and 73.0 ± 0.45 mm in 1999 (Mann-Whitney U test: $U = 932.0$, $P = 0.37$). There was no correlation between mass and time of day ($r = -0.097$, $P = 0.36$) or Julian date ($r = 0.14$, $P = 0.17$). Habitat type was a significant predictor of variation in male body condition (mass divided by wing chord; Table 2), with more heavier, larger males in edge sites than in clear-cuts (Fig. 4).

Nesting success

Collectively, 204 White-throated Sparrow territories were monitored in 1998 and 1999, of which 34.8% successfully fledged young (1998: 38.7%, $n = 106$;

Fig. 2. Histogram showing the distribution of reproductive index values in clear-cut sites (A), edge sites (B), and interior forest sites (C) for 1998 and 1999 combined.
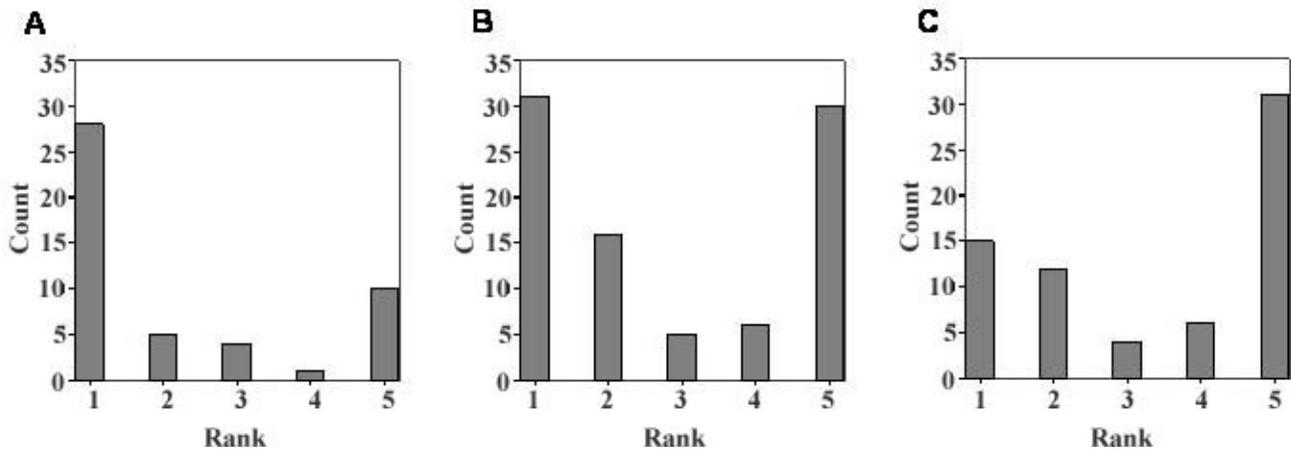
1999: 30.6%, $n = 98$; $X^2 = 1.46$, df $= 1$, $P = 0.23$). The proportion of territories with fledged young was lower in clear-cut sites than in forest edge or interior sites (Fig. 5), and habitat type was a significant predictor of variation in the proportion of territories that successfully fledged young (Table 2).

A total of 31 White-throated Sparrow nests were located in 1998 and 1999. Of these, only eight successfully fledged young (25.8% success); 3 of 17 (17.6%) were successful in edge habitat, 5 of 12 (41.7%) in interior forest, and 0 of two (0%) in clear-cuts.

Sixty-eight percent of 106 territorial males monitored in 1998 and 59% of 98 territorial males monitored in 1999 successfully obtained mates. Habitat type was a significant predictor of male pairing success (Table 2), with higher pairing success in edge and interior forest than in clear-cuts (Fig. 6).

Fledging success, i.e., the average number of fledglings observed within each 10-ha plot, was highest in forest interior plots and lowest in clear-cuts (Fig. 7), and habitat type was a significant predictor of fledging success (Table 2).

Site fidelity

A total of 39.7% of 73 banded adult male White-throated Sparrows returned to the same site occupied in the previous breeding season. Return rates did not differ significantly between males banded in 1998 and those banded in 1999 ($\chi^2 = 0.20$, df $= 1$, $P = 0.66$), with 41.9% of 43 males banded in 1998 returning in 1999 and 36.7% of 30 males banded in 1999 returning in 2000. Rates of male site fidelity were higher in interior forest and edge sites (interior: 44.4% of 27 banded males returned; edge: 41.2% of 34 banded males) than in clear-cut sites (25.0% of 12 banded males). However, habitat type was not a significant predictor of variation in male return rates (Table 2). No banded nestlings ($n = 21$) were observed in the study area in subsequent years.

DISCUSSION

Our results suggest that territory density of White-throated Sparrows was not a useful surrogate for habitat quality in three broad forest habitat types in the boreal mixedwood forest of central Alberta. Although there were significant differences in the territory density of breeding White-throated Sparrows among habitat types, the patterns in density were not consistent with the indices of habitat quality we measured in this study. Despite having the highest density of territories each year,

Fig. 3. White-throated Sparrow territory density (males/10 ha) in recent clear-cuts, forest edges, and interior forest at Calling Lake, Alberta, 1998–1999. Numbers above bars indicate total number of territories. See text for results of linear mixed model analyses.
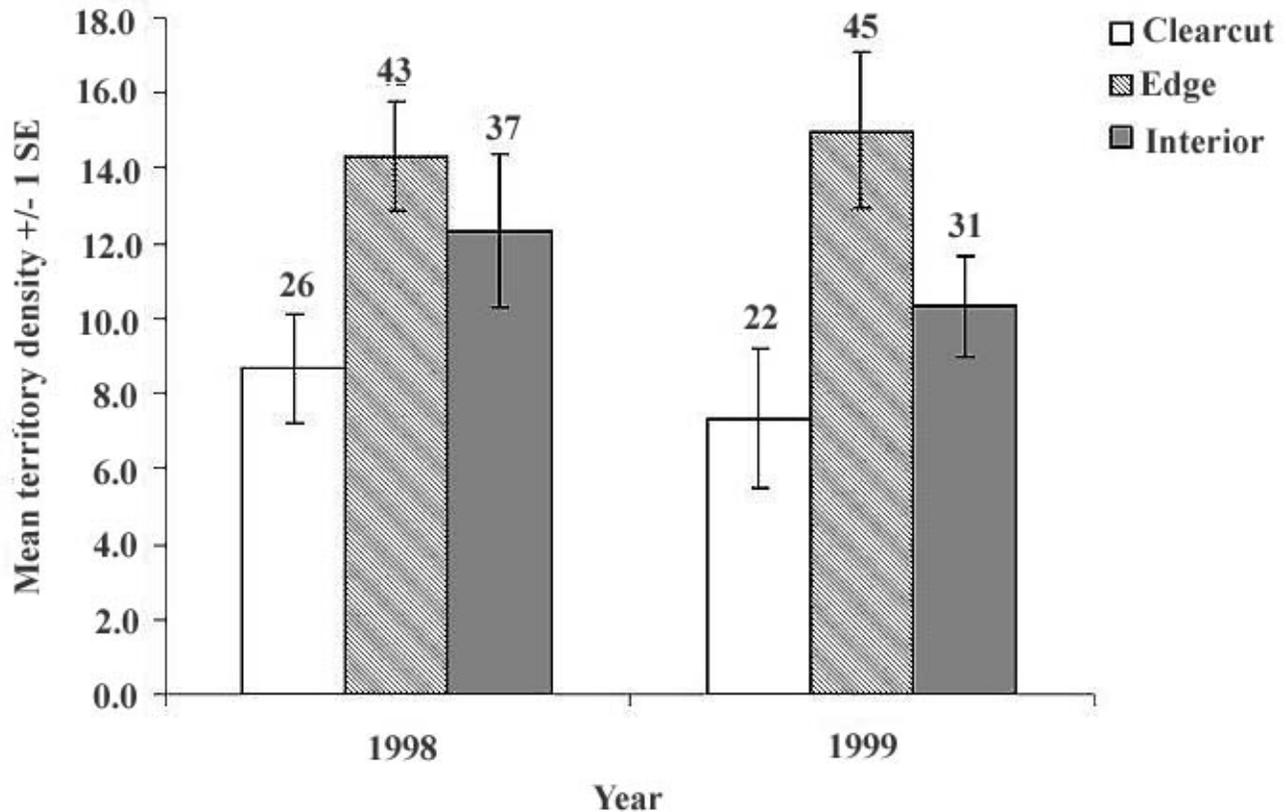
edge sites did not represent the highest-quality habitat in terms of pairing success, nesting success, and fledging success. Based on these indices, clear-cut sites often represented the lower-quality habitat, and interior forest sites appeared to represent higher-quality habitat.

Considering the marked structural differences in the habitat types that we sampled in this study, it is possible that some of the observed patterns were the result of a consistent bias in detectability rather than a true effect. However, we have several lines of evidence to suggest that a bias in detectability was not responsible for the observed differences. White-throated Sparrows often nest, forage, and sing close to the ground (Falls and Kopachena 1994), increasing the probability of encounter rates with human observers. Territory densities were also very

high within the study area, making birds highly vigilant and responsive to territory intrusion. As a result, most birds were also recorded visually, and with more than 60% of territories containing at least one color-marked individual, territory density could be more accurately estimated. Most territorial males are detected when they are singing (Dejong and Emlen 1985), although singing rates are highly variable and often related to an individual bird's pairing status (McShea and Rappole 1997). In this study, male White-throated Sparrows in clear-cuts sang considerably more than birds in edge sites or interior forest (K. C. Hannah, *unpublished data*). Because a higher proportion of males in clear-cuts were unpaired, they should have also been easier to detect than birds in other habitat types in which males had higher rates of pairing success. Therefore, the patterns in territory density and habitat quality

Table 2. Parameter estimates for models explaining variation in territory density (males/10 ha), body condition (weight/wing chord), nest success (based on a reproductive index), pairing success, fledging success (fledglings/10 ha) and site fidelity of White-throated Sparrows in relation to habitat type (clearcut, forest edge, forest interior) near Calling Lake, Alberta, 1998–1999 (1999–2000 for site fidelity). The value t is the result of the independent samples t test; see text for explanation of mixed models analyses used. Parameters were calculated as mean differences in relation to habitat type "clear-cut." For example, a positive estimate for territory density in habitat type "edge" vs. "clear-cut" indicates that territory density was higher in edge plots than in clear-cut plots.

Parameter	Estimate	SE	t	P
Territory density				
Intercept	8.00	1.59	5.04	0.0007
Habitat type ("edge" vs. "clear-cut")	6.67	2.24	2.97	**0.03**
Habitat type ("interior" vs. "clear-cut")	3.33	2.24	1.49	0.19
Body condition				
Intercept	0.35	0.005	64.8	<0.0001
Habitat type ("edge" vs. "clear-cut")	0.01	0.006	1.98	**0.05**
Habitat type ("interior" vs. "clear-cut")	0.008	0.006	1.24	0.25
Nesting success				
Intercept	-1.35	0.38	-3.54	0.0005
Habitat type ("edge" vs. "clear-cut")	0.69	0.46	1.49	0.19
Habitat type ("interior" vs. "clear-cut")	1.18	0.47	2.51	**0.05**
Pairing success				
Intercept	-0.33	0.29	-1.14	0.26
Habitat type ("edge" vs. "clear-cut")	0.95	0.37	2.55	**0.01**
Habitat type ("interior" vs. "clear-cut")	1.60	0.42	3.83	**0.0002**
Fledging success				
Intercept	2.83	2.05	1.38	0.20
Habitat type ("edge" vs. "clear-cut")	6.83	2.90	2.36	**0.06**
Habitat type ("interior" vs. "clear-cut")	9.50	2.90	3.28	**0.02**

| Site fidelity				
Intercept	-1.11	0.73	-1.52	0.13
Habitat type ("edge" vs. "clear-cut")	0.82	0.87	0.94	0.38
Habitat type ("interior" vs. "clear-cut")	0.92	0.88	1.05	0.34

indices observed in this study do not appear to be the result of a systematic bias. In fact, any bias in detectability should have favored birds in clear-cuts. The fact that clear-cuts consistently had lower territory densities and lower scores in most of our measurements of habitat quality further strengthens our suggestion that there was little bias in our results because of detectability.

Although the sequence of male territory settlement may indicate differences in habitat quality, there were no significant patterns in territorial settlement by male White-throated Sparrows among habitat types. White-throated Sparrows are short-distance migrants that arrive on the breeding grounds during a relatively narrow period of time, often settling and establishing territories within the span of only a few days (Knapton et al. 1984, Hannah 2001). Our results suggest that individual White-throated Sparrows were not selecting the highest-quality habitats first, as would be expected based on the ideal despotic model of habitat selection (Fretwell and Lucas 1970, Bernstein et al. 1991). Birds also did not appear to settle in the lowest-quality habitats first, suggesting that male White-throated Sparrows were not selecting ecological traps (Weldon and Haddad 2005). Birds arriving early on the breeding grounds may later be evicted by more dominant individuals or those birds returning to breeding sites from the previous year (Lanyon and Thompson 1986, Jakobsson 1988), thereby decoupling any hypothesized relationship between settlement rate and habitat quality. Also, birds may not recognize inferior habitat types until later in the breeding season following an unsuccessful nesting attempt, at which point they may disperse away from poor-quality territories rather than attempting to nest again under suboptimal conditions (Haas 1998, Doligez et al. 2002). Our observation that rates of territory abandonment by males were higher in clear-cuts than in interior forests or edge sites appears to support this suggestion. Additionally, although differences in the site fidelity of males

were not statistically significant among habitat types, more males returned to edge and interior forest sites than to clear-cut sites, further suggesting that birds may not have correctly assessed habitat quality at the beginning of the breeding season.

Results from studies measuring the impact of forest fragmentation on avian food resources have been equivocal, with some studies suggesting that fragmentation leads to declines in arthropod numbers (Gibbs and Faaborg 1990, Burke and Nol 1998), whereas others suggest that arthropod numbers increase in fragmented landscapes (Didham et al. 1998, Van Wilgenburg et al. 2001). Given the inconsistency of results and the difficulty in accurately sampling arthropods, we compared differences in the body condition of birds between habitat types as an indirect measure of food quantity or quality. In this study, we detected significant differences in male body condition among habitat types: Birds at edge sites were larger and heavier than those in clear-cuts, and birds in interior forest sites were in moderate condition. This result may imply that differences in food resources exist among habitat types or that differences may be a result of male foraging efficiency (Cresswell et al. 2001). Although slight, these minor differences in male body condition could have implications on life history parameters such as adult survival and reproductive success (Arcese and Smith 1988, Bolton et al. 1993). The White-throated Sparrow also exhibits plumage polymorphism, and birds differ both morphologically and behaviorally during the breeding season (Lowther 1961). Larger, more aggressive males may have settled in higher-density edge sites as a means of securing more extra-pair fertilizations, which is a common strategy for these larger males (Formica et al. 2004). Smaller, less aggressive males may seek out lower-density areas in which they are more able to guard mates from intruding neighboring males, possibly explaining the habitat-based variation in the body condition of males observed in this study.

Fig. 4. Mean body condition of male White-throated Sparrows banded in 1998 and 1999 near Calling Lake, Alberta. Body condition was calculated as weight (g) divided by wing chord (mm). Numbers above bars indicate total males. See text for results of mixed model analyses.
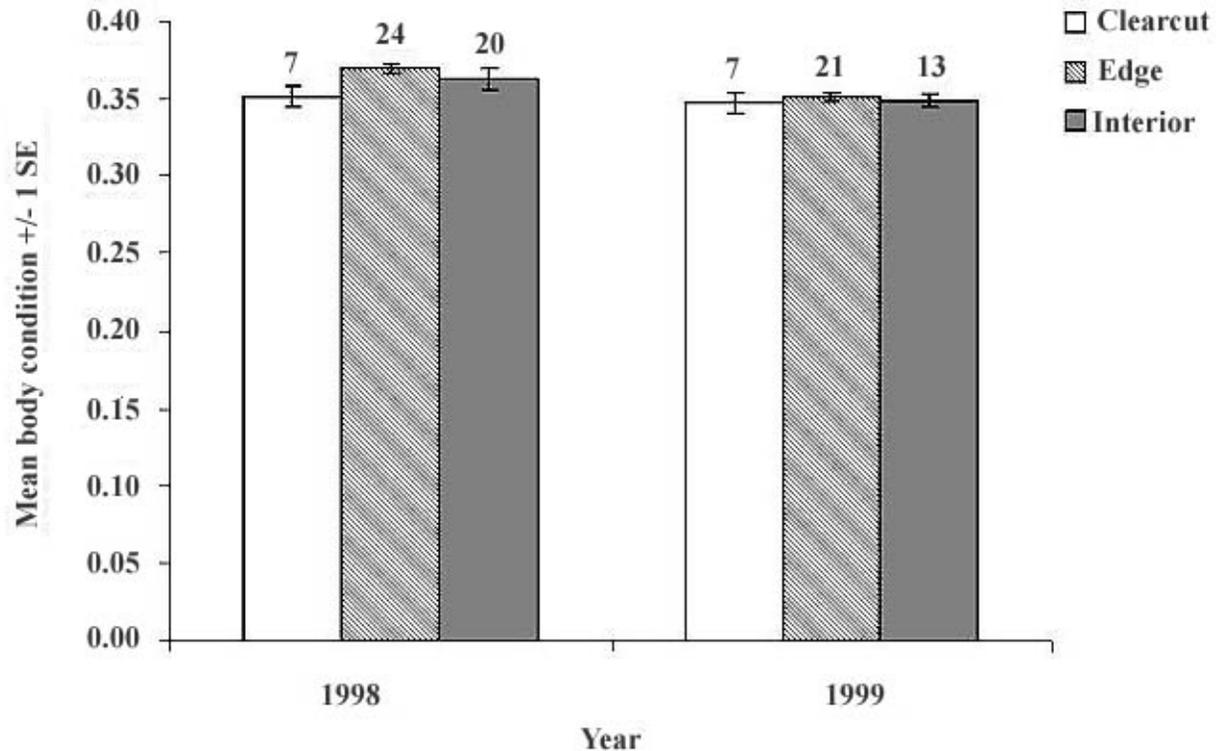

White-throated Sparrow nesting success averaged 25.8% based on monitored nests and 34.8% using a reproductive index; these averages are slightly below rates of nest success recorded for this species in other parts of its breeding range (Knapton et al. 1984, Falls and Kopachena 1994). Although nest predation and parasitism have been implicated in other studies examining fragmentation effects on songbirds, we found no evidence to suggest that these factors were responsible for the low success rates of the monitored nests in this study. Instead, patterns of nesting success may simply reflect differences in rates of male pairing success. Consistent with several other habitat quality indices measured in this study, pairing success was highest in interior forests and lowest in clear-cuts. Variation in male pairing success might suggest a strong male-biased sex ratio or a strong selective pressure by females to mate with males in more intact habitats (Bayne and Hobson 2001, Donovan and Flather 2002, Lampila et al. 2005). Unpaired, nonterritorial "floater" females are known to exist in populations of this species (Falls and Kopachena 1994) and may go undetected in surveys. Floater females in our study may be unwilling to trade off floating in intact habitats for territoriality in marginal habitats in the short term, preferring instead to wait for opportunities as replacement females in an existing higher-quality territory.

Habitat fragmentation is thought to constrain dispersal by birds, ultimately restricting females from accessing males in more patchy or fragmented areas (Bayne and Hobson 2001, Lampila et al. 2005). Although reduced dispersal may limit breeding opportunities for males in highly fragmented areas, the experimental translocation of male White-throated Sparrows in our study region showed no reduction in dispersal capability in patchy habitats (Gobeil and Villard 2002). If

Fig. 5. Proportion of territories with fledged young in recent clearcuts, forest edges and interior forest at Calling Lake, Alberta, 1998-1999. Numbers in bars indicate total number of territories. See text for results of mixed model analyses.
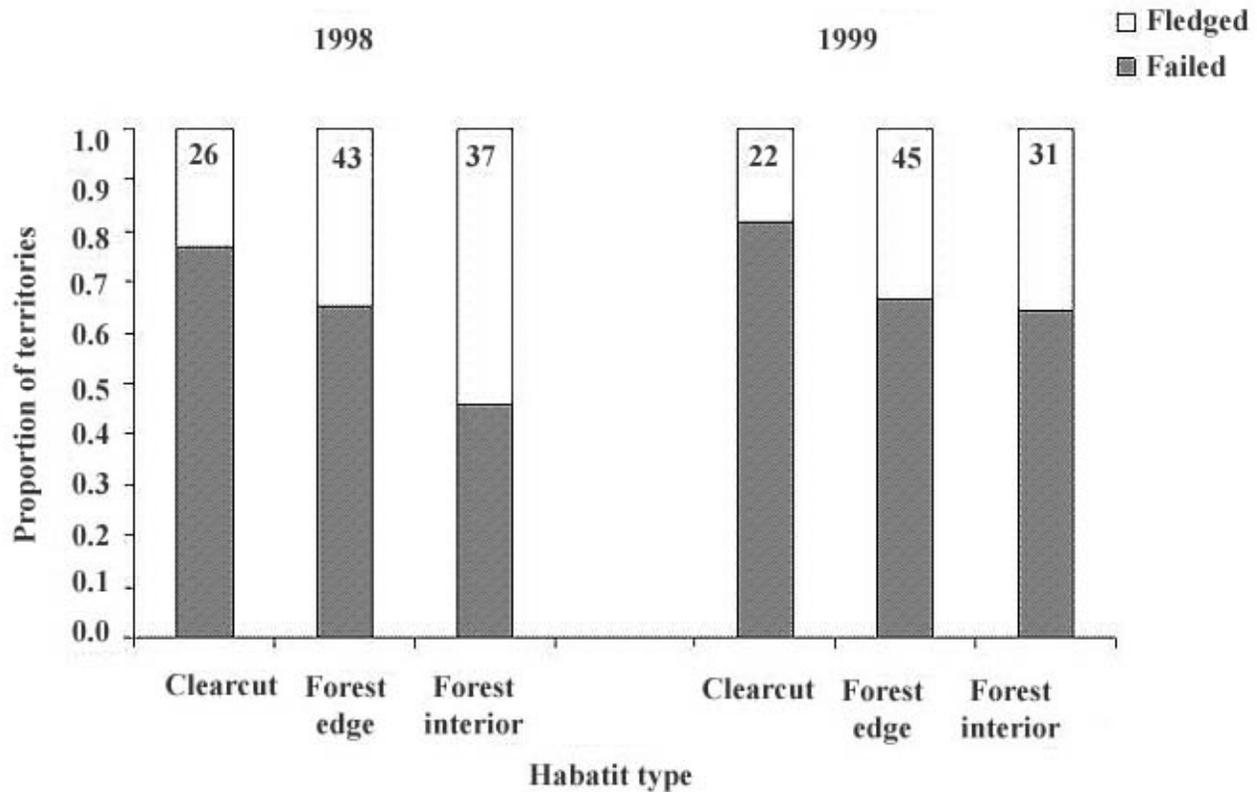

dispersal by females in patchy habitats is not constrained, this suggests that females might simply be opting to mate with males in more intact sites (Lampila et al. 2005), rather than attempting to nest with males in lower-quality habitats. Although we did not test female selection directly, we observed a small number of polygynous matings in edge habitat and one case of polygyny in interior forest (Hannah 2001); this is a rarely observed behavior in an otherwise monogamous species (Falls and Kopachena 1994). Females may have avoided unpaired males in clear-cuts in favor of settling within the territories of paired males in forest edge and interior sites, suggesting that clear-cuts may represent poorer-quality habitat. However, polygyny can be costly, especially if the territorial male provides no parental care and the second female is inexperienced, but this strategy may still be advantageous to late-arriving or less experienced females (Petit 1991). By nesting later than the primary female, secondary females may reduce competition for male assistance and provisioning, thereby reducing the cost of polygyny (Leonard 1990).

Fledging success, or the average number of independent offspring produced, was highest in interior forest sites and lowest in clear-cuts, which was consistent with our observed patterns in nesting success. Based on observed fledging success, none of the sites appeared to contain self-sustaining populations. However, fledging success combined with the relatively high rates of adult site fidelity in interior forest and edge sites indicates that these two habitat types may have been self-sustaining. The low fledging success and male site fidelity in clear-

Fig. 6. Pairing success of territorial males in recent clearcuts, forest edges and interior forest at Calling Lake, Alberta, 1998-1999. Numbers in bars indicate total number of territories. See text for results of mixed model analyses.
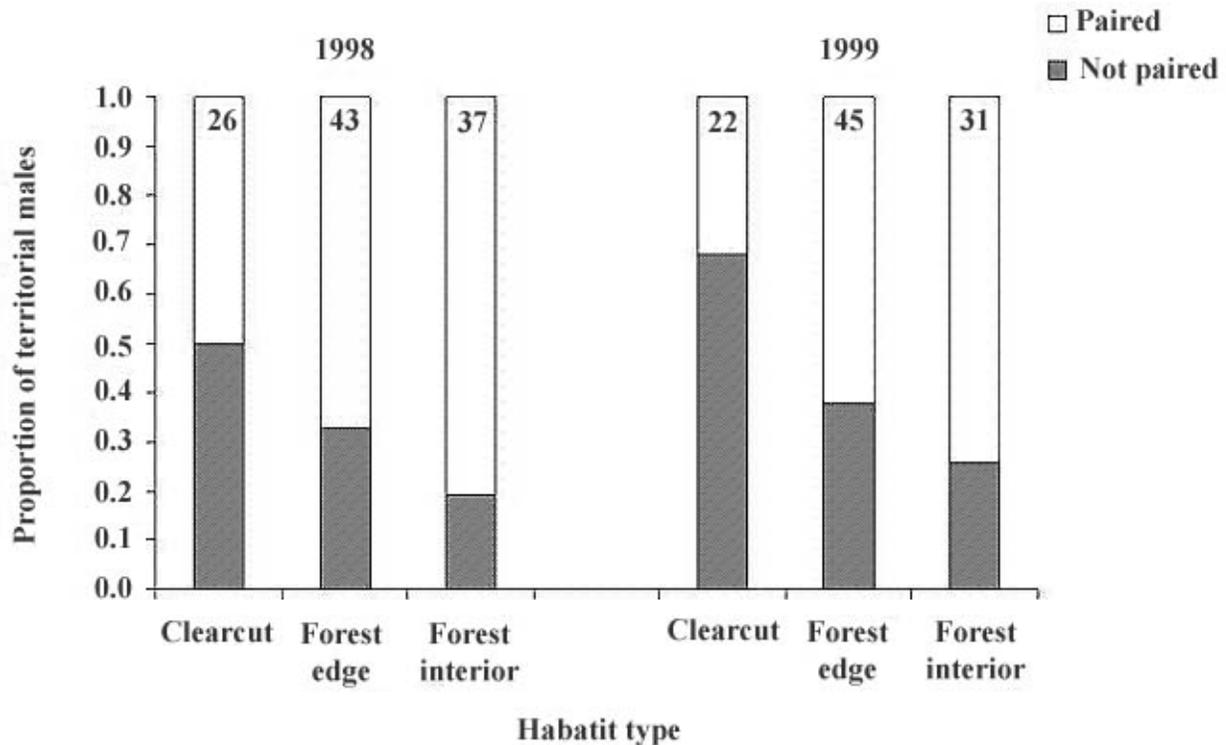

cuts suggest a lack of population sustainability in this habitat type, implying that these populations were maintained by the immigration of birds from elsewhere (Pulliam 1988).

Although White-throated Sparrows rapidly colonize recent clear-cuts (Schieck and Song 2006), our results indicate that habitat quality in these habitats may be quite low, at least in the first few years following the harvest. Bayne and Hobson (2001) suggest that, as clear-cuts regenerate in areas managed for commercial forestry, fragmentation effects may be short-lived, with habitat quality gradually improving and returning to preharvest conditions relatively quickly. However, Rangen et al. (2000) found that White-throated Sparrow density was twice as high and reproductive success nearly four times as high in older forests (75–100 yr) than younger ones (25 yr post-harvest) in west-central Alberta (~300 km west of our study site).

These results suggest that habitat loss and fragmentation effects may persist for a considerable length of time following forest harvesting.

In systems in which large stand-replacing fires were historically the dominant form of disturbance, species may be adapted to large-scale habitat change (Westworth and Telfer 1993, Schieck et al. 1995). Although most research has focused on post-fire responses of primary and secondary cavity nesting birds (Hobson and Schieck 1999, Hoyt and Hannon 2002), responses by the larger breeding bird community following wildfire and subsequent salvage-logging operations are less well known (Schmiegelow et al. 2006). Stambaugh (2003) compared patterns in White-throated Sparrow reproductive success between burned forests, both salvage-logged and unsalvaged, and unburned forests in west-central Alberta ~300 km southwest of our study site. Although he found comparable

Fig. 7. Mean number of fledglings per plot (1 plot = 10 ha) in recent clearcuts, forest edges and interior forest at Calling Lake, Alberta, 1998-1999. Numbers above bars indicate total number of fledglings observed in each plot (based on maximum number of fledglings observed in the presence of adults). See text for results of mixed model analyses.
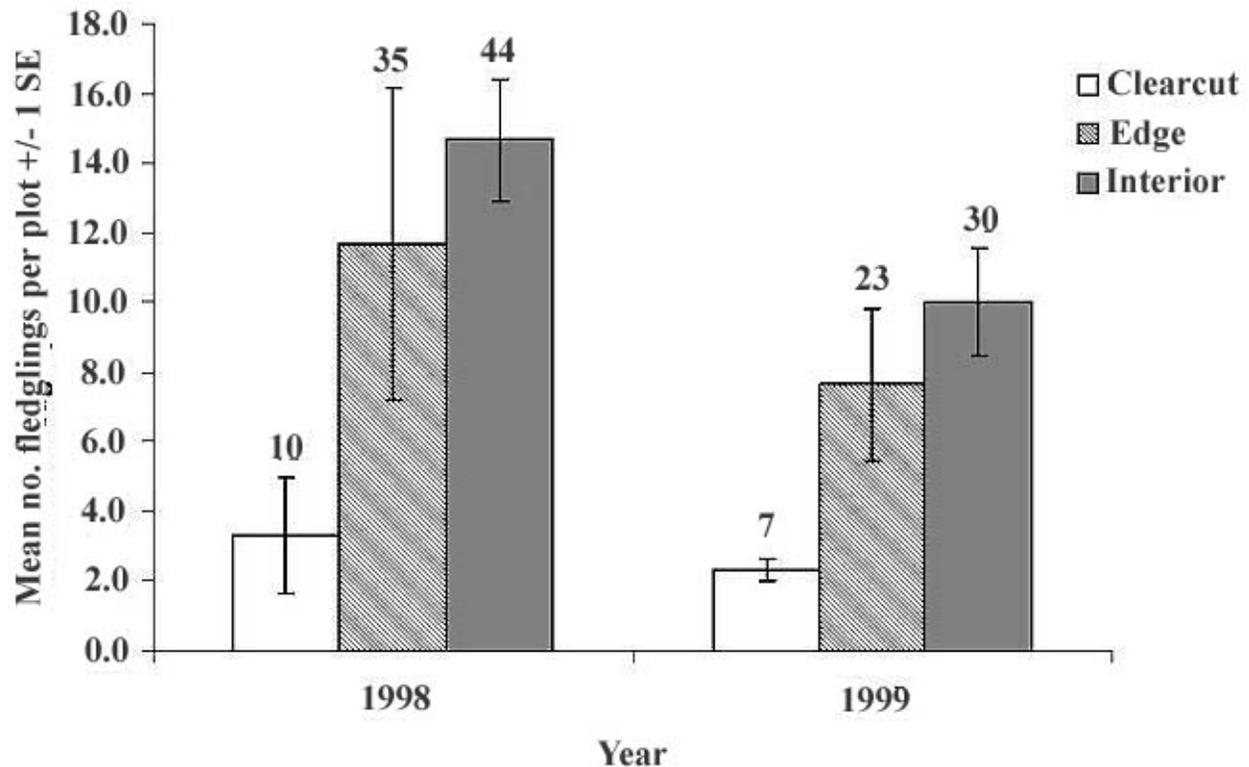
rates of reproductive success between unburned sites and burned unsalvaged sites, White-throated Sparrows in burned salvage-logged sites suffered significantly lower reproductive success. These results suggest that White-throated Sparrows may be more resilient to natural forms of disturbance, such as wildfire, than to anthropogenic disturbances, such as harvesting, and that stands regenerating after harvest may not emulate the conditions that exist following fire. How long stands originating from harvest continue to provide inferior habitat for this species remains unclear, and should be further investigated.

CONCLUSIONS

Simple comparisons of patterns in species density may be insufficient, if not misleading, when used to assess the effects of forest harvesting on birds, including species perceived to be general in their habitat preferences. Patterns in territory density of the White-throated Sparrow were not indicative of the negative impacts of habitat disturbance from forest harvesting on several habitat quality indices. Individuals in clear-cuts were apparently not able to evaluate habitat quality during territory establishment and thereby suffered reduced reproductive success. Some individuals appeared to adjust for this variation in habitat quality later in the breeding season by moving away from poor-quality sites, but it is unclear if these birds were reproductively successful in later re-nesting attempts following dispersal. Based on work in early

post-fire environments, natural disturbances such as wildfires do not reduce habitat quality for this species, at least in the first few years following disturbance (Stambaugh 2003). In contrast, reduced habitat quality in stands following harvesting may persist for decades, until the structural attributes of forests originating from wildfire and harvesting converge (Hobson and Schieck 1999, Schieck and Song 2006). In landscapes heavily fragmented by forestry and other industrial development, the remaining habitat may approach a lower threshold at which rates of recruitment, immigration, and site fidelity are reduced to the extent that local or regional population declines occur. Large-scale surveys, such as the continent-wide Breeding Bird Survey, can potentially be used to identify spatial and temporal patterns in species occurrence and guide more detailed population-level research.

Although debate continues as to the potential mechanisms responsible for declines in many species of North American songbirds (e.g., Holmes 2007), we present the first evidence to suggest that habitat alteration on the breeding grounds may negatively affect White-throated Sparrows. Despite the fact that this species has been the subject of intense genetic and behavioral research (Falls and Kopachena 1994), its high abundance and ubiquitous occurrence have resulted in its being overlooked as the subject of more detailed population-level studies measuring species' responses to habitat alteration. However, conservation interest should also be directed at keeping common species, such as the White-throated Sparrow, common (Dunn 2002), especially because it has been identified as a high conservation priority (Dunn et al. 1999). Our results suggest that this species may be more sensitive to local-scale forest harvesting than previously thought. Harsh weather conditions on the wintering grounds during the mid-1970s may have been responsible for some declines observed in central and eastern Canadian White-throated Sparrow populations (Sauer et al. 1996, Mazerolle et al. 2005), although it seems likely that populations would have rebounded in recent decades if this were the primary mechanism responsible. Activities on the breeding grounds could also be negatively affecting this species, and our results suggest that further study is warranted, particularly in the eastern portions of the breeding range. High rates of current landscape change throughout the western extent of the breeding range also support the need for more careful consideration of research and management needs for the conservation of this species.

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