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Physiological ramifications of habitat selection in territorial male ovenbirds: consequences of landscape fragmentation

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Abstract Since boreal forest fragments are of lower quality than contiguous forest for breeding Ovenbirds (*Seiurus aurocapillus*), we predicted that competition for breeding sites in contiguous forest should lead to a greater prevalence of individuals in better condition in these habitats. We quantified male condition using morphological and hematological indices. Males in contiguous forest were larger than males in forest fragments and had higher hematocrits and mean corpuscular volumes, as well as a greater prevalence of polychromatic cells. These hematological indices are all positively associated with energy demands or stress, or both. Furthermore, the proportion of heterophils, a type of white blood cell positively associated with stress, decreased through the breeding season only for males in forest fragments. Total plasma protein and mass corrected for structural size did not differ between landscapes, suggesting that the nutritional status of males was similar between landscapes. All of these trends were independent of age. Overall, these results indicate that size of male Ovenbirds could be playing a role in habitat selection, but that defending territories in contiguous forest, where breeding success is higher and populations are denser, seems to result in greater energetic demands and a reduced immunological condition. These results demonstrate a physiological component to contrasting consequences associated with territory acquisition in birds.

Keywords · Habitat selection · Hematology · Forest fragmentation · Ideal Despotic · Neotropical migrant

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Introduction

In North America, forest fragmentation can reduce the quality of forested habitats for Neotropical migrant songbirds by altering predator and brood parasite communities (Brittingham and Temple 1983; Paton 1994), vegetation assemblages (Matlack 1993), microclimate (Chen et al. 1993), and food abundance (Burke and Nol 1998; Zannette et al. 2000). Consequently, populations of many songbird species decrease with increasing levels of forest loss and fragmentation (Wenny et al. 1993; Burke and Nol 1998; Mancke and Gavin 2000; Bayne and Hobson, in press). However, little is known about interactions between the condition of individuals, as indicated by morphometric and physiological parameters, and habitat quality as influenced by forest fragmentation. Are males in poorer body condition occupying inferior habitat compared with males in better condition (Marra et al. 1998)?

The Ideal Despotic model (Fretwell and Lucas 1970) has been used to interpret non-random distribution of individual birds among habitats (Holmes et al. 1996; Petit and Petit 1996; Sherry and Holmes 1996). This model predicts that individuals select habitats to maximize their fitness, and that habitat quality decreases as density increases. Because individuals vary in competitive abilities, as intraspecific density increases territoriality is expected to force less competitive individuals from higher-quality habitats, resulting in lower reproductive success (Fretwell and Lucas 1970). Very few studies have examined the demography of songbirds in fragmented and contiguous forest in the context of the Ideal Despotic model of habitat selection.

A previous study in central Saskatchewan, Canada, examining Ovenbirds (*Seiurus aurocapillus*) in fragmented and contiguous boreal forest, demonstrated that male Ovenbirds distribute themselves among landscapes consistent with the Ideal Despotic model of habitat selection (Bayne and Hobson 2001, in press); Ovenbirds in forest fragments had reduced pairing success, lower nesting success, a greater proportion of first-time breeders, lower densities, and lower apparent annual survival than males in contiguous forest. Based on these demographic parameters, Bayne and Hobson (in press) concluded that forest fragments within agricultural landscapes were likely population sinks for breeding Ovenbirds, whereas contiguous forest was probably a population source. Because habitat quality appears superior for Ovenbirds breeding in contiguous boreal forest, we reasoned that competition for these areas should be intense. Consequently, individuals in better body condition should be more prevalent in contiguous forest than in forest fragments.

Our primary objective was to assess whether measures of physiological condition and size of male Ovenbirds were related to patterns of male distribution within fragmented and contiguous boreal forest. Secondly, we determined whether habitat quality influenced the condition of territorial male Ovenbirds by contrasting variation in condition indices throughout the breeding season in forest fragments and contiguous forest. Hematological indices used in this study included hematocrit (Hct), total red blood cell (RBC) count, mean corpuscular volume (MCV), total plasma proteins (TPP), RBC polychromasia, total white blood cell (WBC) count, percentage of heterophils, percentage of lymphocytes, and differential ratios (i.e., percentage of heterophils/percentage of lymphocytes).

Background on body condition indices

Blood parameters are increasingly being used to quantify sub-lethal effects of various stressors or environmental conditions on the health of many organisms (e.g., Maxwell et al. 1991; Hellgren et al. 1993; Hõrak et al. 1998; Ots et al. 1998). Background information on hematological parameters used in this study, as well as the reasoning behind their predicted responses are provided below.

Hct consists of the proportional volume of RBCs in the total blood volume. Increases in Hct are often associated with increases in oxygen-carrying capacity (Campbell 1995). Alternatively, Hct levels can also increase through dehydration, as a result of a reduction in the volume of plasma, or decrease through anemias, which can result from conditions such as starvation, dehydration, parasite infections, or hemolytic diseases (Campbell 1995). Consequently, variation in Hct can be difficult to interpret, and its use as an index of condition is somewhat controversial (Dawson and Bortolotti 1997a). Mean cell volume (MCV), which is derived from total RBC count and Hct values, clarifies whether variation in Hct values is a result of changes in the number or size of cells (Campbell 1995). Recently, Bearhop et al. (1999) found that MCV of healthy male Great Skuas (*Catharacta skua*) was negatively correlated with their reproductive success. In addition, a study on Black Bears (*Ursus americanus*) found that MCV values were lower in years with abundant, high-quality forage (Hellgren et al. 1993). RBC polychromasia is an index of the abundance of larger, immature RBCs (Campbell 1995). Previous studies on birds have detected significant increases in the abundance of polychromatic cells as a result of stress (Heppel and Kornberg 1946; McKilligan 1996). Since forest fragments seem to consist of lower-quality breeding habitat than contiguous forest, we predicted that Ovenbirds in forest fragments should be more stressed than birds in contiguous forest. Consequently, individuals in forest fragments should have higher Hct values, higher MCV values and more polychromatic cells than birds in contiguous forest.

TPP values provide a measure of the amount of proteins in blood plasma (Campbell 1995). Plasma proteins play an important role in the preservation of blood volume and in the maintenance of an optimal blood pH (Sturkie 1976), and they often decrease in response to stress (Sturkie 1976) and vary with diet quality (Gavett and Wakeley 1986). Several studies have reported relationships between plasma proteins and residual mass (mass corrected for structural size) and have suggested that TPP is often related to the nutritional status in animals (Messier et al. 1987; de le Court et al. 1995; Dawson and Bortolotti 1997b). Alternatively, TPP values can also increase in response to infections as a result of the secretion of proteins transporting antibodies (De Lope et al. 1998). Since the birds used in this study were visibly healthy and levels of blood parasitism were low (Mazerolle, unpublished data), we interpreted TPP as an indicator of nutritional status. As forest fragments seem to consist of lower-quality breeding habitat compared to contiguous forest, we predicted that Ovenbirds in forest fragments should have lower TPP and residual mass values than Ovenbirds in contiguous forest.

Increases in heterophils/lymphocyte ratios have been positively associated with numerous stressors (Maxwell 1993; Ots and Hõrak 1996, 1998; Moreno et al. 1998). Elevated percentages of heterophils are indicative of stress, whereas deficiencies in lymphocytes are often indicative of immunosuppression and result in an increased susceptibility to viral infections (Siegel 1985; Maxwell 1993). Thus, we predicted that Ovenbirds in forest fragments should have a lower proportion of lymphocytes and a higher proportion of heterophils than Ovenbirds in contiguous forest.

Materials and methods

Study area

Our study was conducted in the southern boreal mixedwood forest of central Saskatchewan (53°50′N, 105°50′W). Ovenbirds were sampled in Prince Albert National Park (PANP), a contiguous forest area of approximately 387,500 ha, and in an adjacent rural municipality where approximately 70% of the land area is agricultural fields and 23% is forested (Bayne and Hobson 1997). Ovenbirds were sampled in mature stands dominated by trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*). Individuals were captured in 10 forest fragments and 6 contiguous forest stands (1–5 individuals per site). Forest fragments sampled in the agricultural landscape ranged from 9 to 40 ha. All sites were at least 2 km apart.

Field techniques

Male Ovenbirds were captured using song playback to draw birds into mistnets. All birds were captured between 23 May and 24 June 2000, coinciding with the period of peak territoriality. Mass and morphological measurements such as bill length, bill width, flattened right wing length, tail length and right tarsus length were measured following the methods outlined in Pyle (1997). The author, D.F.M., took all measurements. The average of two measurements of each morphological attribute was used in all analyses. Sex was determined using occurrences of brood patch or cloacal protuberance (Pyle 1997). Age was determined using a modification of the Donovan and Stanley's (1995) method as described in Bayne and Hobson (2000). A bird was classified as second-year (SY) if the angle formed by the tip of the 3rd rectrix was <84° and as an after-second-year (ASY) when >84%.

Blood sampling

All blood samples (100–125 ul) were collected between 0530 hours and 1730 hours within 5 min of capture using standard hematological methods outlined in Campbell (1995). All samples were collected from the brachial vein with a 27-gauge needle and were processed within 6 h of collection. Hematocrits were determined by centrifuging blood in micro-hematocrit tubes for 10 min at 10,000 rpm in a clinical centrifuge (IEC-428 model, International Equipment, Mass., USA). TPP were determined using a clinical refractometer (A300CL model, Atago, Tokyo, Japan). Because TPP becomes concentrated as plasma volume decreases (Pearson correlation, $r=-0.335$, $n=60$, $P=0.009$), we quantified the density of plasma proteins by using the residuals of a linear regression with plasma volume versus TPP. RBC were calculated with an improved Neubauer hemacytometer (1483 model, Hausser Scientific, Pa., USA) using the red blood cell Unopettes for staining and dilutions (Unopette test 5850/5851, Becton, Dickinson, N.J., USA). MCV values were calculated using the formula outlined in Campbell (1995).

For quantifying WBC and RBC polychromasia, a thin coat of blood was smeared on a microscope slide, air-dried, fixed in absolute ethanol and stained with Wright-Giemsa solution. Individuals in the Clinical Pathology Laboratory at the Veterinary College of the University of Saskatchewan examined all blood smears. The proportion of different types of leukocytes was determined by examining 100 white blood cells. The total number of white blood cells was estimated by counting the number of WBC per field at 500× and using a modification of the formula described in Lane (1996). Finally, RBC polychromasia was determined by counting the number of polychromatic cells per field at 1,000×.

Statistical procedures

Because very few (1–5) individuals were sampled per site, it was not possible to examine or control for site characteristics such as patchsize and isolation. However, sites that were sampled were representative of the large majority of fragments in this agricultural-forest matrix (Bayne and Hobson, in press).

Principal component analysis (PCA) was computed from a correlation matrix using all morphological measurements (Rising and Somers 1989). The first principal component (PC1) from this analysis was used as an index of structural size. PC1 accounted for 38% of the overall variance, and was characterized by the following morphological parameters and factor loadings: bill length, 0.138; bill width, 0.198; tail length, 0.884; tarsus length, 0.546; wing length, 0.862. PC1 explained more variation in mass of male Ovenbirds than any univariate measure of size. Residual mass was determined by computing the residuals of a linear regression using PC1 as a predictor of body mass. The assumption of linearity between size and mass was examined by comparing higher-order relationships with partial *F*-tests. We also compared residual mass indices computed from the linear regression of PC1 versus mass with the residuals from a reduced major axis regression (RMA), as suggested by Green (2001).

General linear models (GLM) were used to compare blood and morphological parameters between age and landscape treatments for all parameters, except RBC polychromasia. Logistic regression (Norušis 1990) was used to determine the influence of age and landscape on the presence or absence of significant amounts of polychromatic cells (>10 polychromatic cells per field at 1,000×). The prevalence of polychromatic cells was not analyzed as a continuous variable because of the dichotomous scoring used by the Clinical Pathology Laboratory at the Veterinary College of the University of Saskatchewan. A 2×2 contingency table was used to evaluate differences in age structure between landscapes. Pearson correlations were used to examine the association between time of day and date on all condition indices. When time of day or date was correlated with response values, they were added as covariates in GLM analyses using type III sums of squares.

Prior to all analyses, data were tested for normality using 1-sample Kolmogorov-Smirnov tests and for homogeneity of variance using Levene's test (Zar 1996). All statistical analyses were performed with SPSS version 9.0 and were considered significant at an alpha level of 0.05.

Results

All variables were normally distributed (Kolmogorov-Smirnov test, $P>0.05$) and were homogeneous among treatments (Levene's test, $P>0.05$), except TPP and WBC count, which were subsequently log-transformed to improve normality and homogeneity of variance (Zar 1996). Morphology, age, and residual mass of 92 male Ovenbirds were measured, and blood parameters of 65 individuals were quantified, although some samples were incomplete. Our analyses do not focus on blood parasites because their prevalence was extremely low. Two of the 65 males were infected with moderate to low numbers of *Haemoproteus*, and three additional males were potentially infected with moderate to low numbers of unidentified intracellular parasites.

Hematocrit and MCV values were higher in birds in contiguous forest than birds in forest fragments (Tables 1, 2). The proportion of male Ovenbirds with significant amounts of polychromatic cells (more than 10 per field at 1,000×) was significantly greater in contiguous forest than in forest fragments (contiguous forest, $n=36$, 69%; forest fragments, $n=30$, 37%; $P=0.009$). Total RBC counts, TPP, body mass, residual mass and WBC parameters did not differ between landscapes ($P>0.10$). However, both SY and ASY birds were structurally larger, based on the multivariate measure of size and tarsus length, in the contiguous forest than in forest fragments ($P<0.05$). As higher-order polynomial models were not statistically significant (partial *F*-test, $P>0.40$), the relationship between mass and size (PC1) in male Ovenbirds is best described by a linear function ($b=0.374\pm0.098$ [SE], $t=0.827$, $n=90$, $P<0.001$). Residuals computed from the ordinary least squares regression and from the RMA were highly correlated (Pearson correlation; $r=0.829$, $P<0.001$), and results were similar using residual indices computed by both analyses. That is, condition indices computed by both analyses did not differ in relation to male Ovenbird age or landscape use ($P>0.10$).

Table 1 Condition indices and structural size for second year (*SY*) and after-second year (*ASY*) male Ovenbirds in fragmented and contiguous boreal forest. *Hct* Hematocrit, *RBC* total red blood cell counts, *MCV* mean corpuscular volume, *TPP* total plasma proteins, *Residual mass* mass corrected for structural size, *WBC* total white blood cell count

Condition indices	Age	*n*	Contiguous forest		*n*	Forest fragments	
			Mean±SD	Range		Mean±SD	Range
RBC (10^6/mm^3)	SY	15	4.22±1.11	(2.45–6.07)	17	4.27±0.71	(2.70–6.07)
	ASY	21	4.15±0.67	(2.73–4.95)	12	4.25±0.54	(3.11–4.92)
Hct (%)	SY	15	54.8±5.03	(44.50–65.5)	15	52.9±2.91	(47.2–58.5)
	ASY	20	54.2±2.51	(50.3–58.7)	12	51.2±2.88	(47.8–58.2)
MCV (fl)	SY	15	136.8±30.07	(94.2–196.5)	15	127.0±23.74	(89.8–190.6)
	ASY	20	135.9±29.06	(105.4–205.6)	11	122.7±16.15	(103.0–154.3)
TPP (g/100 ml)	SY	15	3.59±0.54	(2.60–4.50)	14	3.48±0.60	(2.80–4.80)
	ASY	19	3.38±0.30	(2.60–3.70)	12	3.26±0.44	(2.60–4.20)
Size	SY	29	–0.06±0.85	(–2.13–1.58)	22	–0.46±0.99	(–2.18–2.28)
	ASY	22	0.46±0.92	(–1.68–2.34)	17	0.04±1.16	(–2.31–2.28)
Residual mass	SY	26	–0.05±1.01	(–1.49–1.99)	22	0.06±0.94	(–.97–2.35)
	ASY	22	0.01±0.76	(–1.54–1.04)	17	–0.01±0.71	(–1.19–1.63)
Lymphocytes (%)	SY	14	62.43±11.93	(44.00–85.00)	16	73.19±13.69	(50.00–94.00)
	ASY	21	66.24±12.51	(41.00–86.00)	13	71.85±11.31	(54.00–88.00)
Heterophils (%)	SY	14	11.07±8.00	(3.00–27.00)	16	11.31±6.19	(4.00–26.00)
	ASY	21	13.76±5.64	(3.00–26.00)	13	10.23±5.85	(1.00–23.00)
Differential ratio	SY	14	0.18±0.14	(0.07–0.45)	16	0.17±0.13	(0.04–0.52)
	ASY	21	0.22±0.13	(0.04–0.63)	13	0.15±0.10	(0.01–0.40)
WBC (10^9/l)	SY	15	2.48±2.66	(0.25–10.50)	17	3.07±2.78	(0.25–9.00)
	ASY	21	2.74±1.71	(0.50–6.00)	13	4.12±2.46	(0.50–9.00)

Table 2 Results from general linear models examining the influence of age and landscape on size and condition indices of male Ovenbirds in fragmented and contiguous boreal forest. *Hct* Hematocrit, *RBC* total red blood cell counts, *MCV* mean corpuscular volume, *TPP* total plasma proteins, *Residual mass* mass corrected for structural size, *WBC* total white blood cell count

		Size	Residual mass	TPP	Hct	RBC	MCV	WBC	Lymphocytes	Heterophils	Differential ratio
Age	*F*	6.14	0.01	3.47	1.44	0.83	2.53	0.10	0.27	0.15	0.13
	P	0.015	0.957	0.068	0.235	0.366	0.117	0.919	0.606	0.703	0.723
	df	1,87	1,87	1,56	1,59	1,60	1,56	1,61	1,59	1,59	1,59
Landscape	*F*	4.10	0.10	1.16	7.77	0.58	4.83	1.52	2.95	0.79	0.426
	P	0.046	0.734	0.285	0.007	0.449	0.032	0.222	0.091	0.377	0.516

SY birds were structurally smaller and tended to have higher TPP than ASY birds whereas all other variables were similar among age groups (Table 2). Wing and tail lengths were responsible for differences in structural size between age groups, both being larger in ASY males than in SY males (*t*-test, t=–2.99, n=90, P=0.004 and t=–2.03, n=88, P=0.046, respectively). However, skeletal measurements (bill width and bill and tarsus lengths) did not differ between age groups (P>0.10).

The proportion of SY males did not differ between landscapes (P=0.660). Overall, 58% and 57% of all individuals were SY birds in fragmented and contiguous forests, respectively. The proportion of SY males in both landscapes differed slightly (59% SY birds in contiguous forest and 65% SY in forest fragments) when the more stringent aging criteria suggested by Donovan and Stanley (1995) were used. However, differences in age structure using these data were still not significant (P=0.605). We found no interaction between landscape and age for any of the condition indices, and the landscape differences in physiology and size detected in this study are independent of age.

Total RBC counts were negatively correlated, whereas MCV, residual mass, proportion of heterophils, differential ratios and WBC were positively correlated with time of day (Table 3). TPP, proportion of lymphocytes and WBC were positively correlated with date, whereas total RBC counts, proportion of heterophils and differential ratios were negatively correlated with date (Table 3).

To determine if condition indices were influenced by habitat quality or if individuals in better condition selected higher-quality habitats, interactions between date and landscape were examined for all condition indices. None of the interactions between date and habitat quality were significant for any of the condition indices (P>0.299), except percentage of heterophils ($F_{1,60}$=4.17, P=0.046). Percentages of heterophils did not vary with date for male Ovenbirds defending territories in contiguous forest

Table 3 Summary of Pearson correlations between condition indices of territorial male Ovenbirds and time of day and date. *Hct* Hematocrit, *RBC* total red blood cell counts, *MCV* mean corpuscular volume, *TPP* total plasma proteins, *Residual mass* mass corrected for structural size, *WBC* total white blood cell count

Health indices	*n*	Time of day		Date	
		r	*P*	*r*	*P*
Hct (%)	62	–0.081	0.534	–0.046	0.725
RBC (10^6/mm^3)	65	–0.251	0.044	–0.265	0.033
MCV (fl)	61	0.266	0.038	0.244	0.058
TPP (g/100 ml)	60	–0.006	0.965	0.372	0.003
Residual mass	91	0.267	0.010	0.196	0.061
Lymphocytes (%)	64	–0.192	0.129	0.513	<0.001
Heterophils (%)	64	0.355	0.004	–0.274	0.029
Differential (%)	64	0.348	0.005	–0.350	0.005
WBC	66	0.452	<0.001	0.288	0.019

(r=–0.001, n=35, P>0.50) but decreased significantly with date for birds in forest fragments (r=–0.567, n=29, P=0.001).

Discussion

Several hematological and morphological parameters differed between male Ovenbirds in contiguous forest and forest fragments. No evidence suggested that SY birds were in poorer condition as a result of having territories in forest fragments. In fact, we found evidence suggesting that, regardless of age, individuals in contiguous forest were more stressed than those in forest fragments, as indicated by Hct, MCV, and RBC polychromasia and the proportion of heterophils. Overall, then, our data clearly indicate a potential physiological consequence to birds reproducing in higher-quality habitat, consequences that in the future must be evaluated in the context of reproductive success and survival.

Landscape and size

Results supported our a priori prediction that male Ovenbirds would be structurally larger in the contiguous forest than in forest fragments. However, it is unclear whether these landscape-differences in structural size are due to larger birds arriving earlier on breeding grounds and preferentially establishing territories in contiguous forest (Francis and Cooke 1986; Marra et al. 1998), or as a result of larger birds actively excluding smaller birds from these habitats, irrespective of arrival dates (Nolan 1978; Lanyon and Thompson 1986). Alternatively, if Ovenbird populations in contiguous forest return to their natal habitats, individuals in contiguous forest could be larger as a result of being raised in higher-quality habitats (Ulfstrand et al. 1981). Future studies should focus on spring settlement and natal philopatry patterns to identify causal mechanisms responsible for size differences in male Ovenbirds among fragmented and contiguous forest. Furthermore, it remains unclear whether there is a direct relationship between structural size and fitness.

Landscape and energetic indices

In contrast to our initial prediction, males in contiguous forest had hematological indices that indicated they were exposed to greater energy demands than males in forest fragments. We found that Hct values of male Ovenbirds in contiguous forest were higher than those of males defending territories in forest fragments. Male Ovenbirds in the contiguous forest also had higher MCV values and a greater prevalence of polychromatic cells than males in forest fragments. Proximate factors responsible for these responses could be higher energetic demands associated either with higher reproductive effort or with defending territories in denser populations found in contiguous forest. Unfortunately, we have no information on reproductive effort or success of focal birds in both landscapes. Previous studies have demonstrated that territorial aggression and levels of testosterone often increase with density of conspecifics (Wingfield and Hahn 1994; Zuk 1996). Since androgens such as testosterone can also increase levels of erythropoiesis (Sturkie 1976), the effects of higher levels of testosterone for males in contiguous forest would also be consistent with our results. Although we did not measure breeding success of the birds that were sampled, Bayne and Hobson (2001) demonstrated that average breeding success of male Ovenbirds in the same study area was higher for males defending territories in contiguous forest than in forest fragments. If this were true also during our study, our findings are consistent with those of Hõrak et al. (1998), who associated an increase in Hct with increased reproductive efforts for Great Tits (*Parus major*) subjected to experimental increases in brood sizes.

Landscape and nutritional status indices

We predicted that males in contiguous forest would be in better nutritional condition than males in forest fragments. However, TPP and residual mass, two indices commonly used as indicators of nutritional status, did not differ for male Ovenbirds sampled in the two landscapes. Previous studies have shown that forest fragmentation can reduce the abundance of arthropods available to forest songbirds (Burke and Nol 1998; Zannette et al. 2000). If food was more abundant or of higher quality in contiguous forest, it is possible that such benefits were offset by increased energetic demands associated with greater reproductive efforts. However, compared with other biomes, fragmentation of boreal forest may have less consequence to songbird food supply because forest arthropods are abundant during the breeding season and any reductions caused by fragmentation may not be sufficient to lower foraging success of songbirds (reviewed by Martin 1987). Insect samples collected in Ovenbird territories in 1999 and 2000 did not indicate any apparent landscape differences in arthropod biomass in fragmented and contiguous forest (Mazerolle and Hobson, unpublished data).

Landscape and immunological indices

We predicted that males in contiguous forest would have a better immunological condition than those in forest fragments. Although mean percentage of heterophils, lymphocytes, and differential ratios did not vary with landscape, there was a significant interaction between date and percentage of heterophils. Percentage of heterophils decreased significantly only for males in forest fragments. As a result, males in forest fragments appeared to finish the breeding season in superior immunological condition relative to males in contiguous forest. Such differences in immunological condition of male Ovenbirds across landscapes could be due to higher reproductive efforts of males in contiguous forest (Ots and Hõrak 1996), or because of a suppression of the immune system of these birds caused by increased levels of testosterone (Zuk 1996).

Temporal variation in blood indices

Unlike Dawson and Bortolotti (1997a), we did not find any variation in Hct with time of day, although we did find that RBC numbers decreased with time of day. As the metabolism of birds is much lower at night, the deterioration and removal of RBCs would be expected to occur at slower rates (Dawson and Bortolotti 1997a). Consequently, the negative correlation in RBC numbers with time of day could be associated with an increase in deterioration and removal of RBCs. We also found that total WBC counts and differential ratios increased during the day. Factors responsible for this pattern are poorly understood, but they could potentially be linked to daily variation in testosterone levels as it is well known that testosterone can adversely influence the immunology of birds (Zuk 1996).

Both TPP and residual mass tended to increase with date indicating that the nutritional status of male Ovenbirds improved during the breeding season. Total WBC counts also increased, whereas differential ratios decreased during this period. These results indicate that the immunological condition of males also improved with date. Hct did not vary with date for male Ovenbirds, although total RBC counts decreased with date. The physiological requirements of migration should act as a strong selection pressure for an enhanced oxygen carrying capacity (Morton 1994). Therefore, reductions in RBCs observed in this study may result from a reduced need for the oxygen uptake capacity during the post-migration period. Overall, all condition indices covaried with date at similar rates in both landscapes, except percentage of heterophils (see previous section).

Age and condition indices

Hematological parameters were similar among age groups, although SY males tended to have higher TPP. Factors responsible for these variations in TPP among age groups are unclear for our results contrast with those of other studies examining species like American Kestrels (*Falco sparverius*) (Dawson and Bortolotti 1997b) and House Sparrows (*Passer domesticus*) (Gavett and Wakeley 1986). Differences between studies could be due to variation in diets among age groups. Alternatively, plasma proteins, such as gammaglobulins, also increase in relation to parasitism as a result of anti-parasite responses (De Lope et al. 1998). Therefore, age effects on TPP could also be related to age-dependent exposure to parasites or other diseases.

Many studies have found age-specific assortments of individuals across habitats of varying quality, whereby older males occupy higher-quality habitats (Holmes et al. 1996; Petit and Petit 1996; Bayne and Hobson, in press). On our study sites, Bayne and Hobson (in press) sampled male Ovenbirds over 4 years and found that the average proportion of SY males was 10% greater in forest fragments than in contiguous forest. In this study, birds were sampled on some of the same sites sampled by Bayne and Hobson (in press), in addition to other nearby sites with similar vegetation, yet we found no significant difference in age-structure between contiguous and fragmented boreal forest. Clearly, age structure among habitats changes seasonally and is linked to other factors, including those influencing population dynamics. In the studies of both Bayne and Hobson (in press) and Holmes et al. (1996), the proportion of SY males in high- and low-quality habitats varied from year to year, and during certain years, age structures were similar across habitats. Currently, the influence of yearly variation in age structure on condition indices of male Ovenbirds in contiguous and fragmented is unknown.

Conclusion

Results from hematological indices indicate that the physiology of male Ovenbirds is associated with habitat selection among fragmented and contiguous boreal forest. Ideal models of habitat selection predict that habitat quality decreases as density of conspecifics increases (Fretwell and Lucas 1970; Morris 1989). Our results, which associate a measurable physiological consequence to defending territories in high-density habitats, support this prediction. However, differences in reproductive success between the two landscapes could also be responsible for these physiological differences. Our findings also provide a potential mechanism for density-dependent habitat selection in songbirds by demonstrating a physiological component to contrasting costs and benefits associated with territory acquisition in birds. It is not clear whether differences in hematological parameters measured here have ultimate fitness consequences for individuals since, to our knowledge, no demographic measures have yet been related to actual costs being paid between males breeding in contiguous versus fragmented forests. Future studies using experimental manipulations to alter densities of conspecifics and reproductive success, paired with the quantification of condition indices, would clarify the physiological costs associated with higher intraspecific competition and breeding success that takes place in preferred habitats. Studies directly examining condition indices during and after habitat selection would also be very informative for determining if habitat quality directly influences the condition of males.

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References

Bayne EM, Hobson KA (1997) Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. Conserv Biol 11:1418–1429

Bayne EM, Hobson KA (2001) Effects of habitat fragmentation on pairing success of Ovenbirds: the importance of male age and floater behavior. Auk 118: 380–388.

Bayne EM, Hobson KA (in press) Apparent survival and source-sink dynamics of Ovenbird populations in fragmented and forested boreal landscapes. Ecology

Bearhop S, Griffiths R, Orr K, Furness RW (1999) Mean corpuscular volume (MCV) as a measure of condition in birds. Ecol Lett 2:352–356

Brittingham MC, Temple SA (1983) Have cowbirds caused forest songbirds to decline? BioScience 33:31–35

Burke DM, Nol E (1998) Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. Auk 115:96–104

Campbell TW (1995) Avian hematology and cytology. Iowa State University Press, Ames

Chen J, Franklin JF, Spies TA (1993) Contrasting microclimate among clearcut, edge, and interior of old-growth Douglas-fir forest. Agric For Meteorol 63:219–237

Court C de le, Aguilera E, Recio F (1995) Plasma chemistry values of free-living white spoonbills *Platalea leucorodia*. Comp Biochem Physiol 112A:137–141

Dawson RD, Bortolotti GR (1997a) Are avian hematocrits indicative of condition? American kestrels as a model. J Wild Manage 61:1297–1306

Dawson RD, Bortolotti GR (1997b) Total plasma protein level as an indicator of condition in wild American kestrels *Falco sparverius*. Can J Zool 75:680–686

De Lope F, Møller AP, De la Cruz C (1998) Parasitism, immune response and reproductive success in the house martin *Delichon urbica*. Oecologia 114:188–193

Donovan TM, Stanley CM (1995) A new method of determining Ovenbird age on the basis of retrix shape. J Field Ornithol 66:247–252

Francis CM, Cooke F (1986) Differential timing of spring migration in wood warblers Parulinae. Auk 103:548–556

Fretwell SD, Lucas HL (1970) On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor 14:16–36

Gavett AP, Wakeley JS (1986) Blood constituents and their relation to diet in urban and rural House Sparrows. Condor 88:279–284

Green AJ (2001) Mass/length residuals: measures of body condition or generators of spurious results? Ecology 82:1473–1483

Hellgren EC, Rogers LL, Seal US (1993) Serum chemistry and hematology of black bears: physiological indices of habitat quality or seasonal patterns? J Mammal 74:304–315

Heppel LA, Kornberg A (1946) Influence of iron salts on the toxicity of lead. Proc Exp Soc Biol Med 61:220–223

Holmes RT, Marra PP, Sherry TW (1996) Habitat-specific demography of breeding black-throated blue warblers *Dendroica caerulescens*. J Anim Ecol 65:183–195

Hõrak P, Ots I, Murumagi A (1998) Haematological health state indices of reproducing Great Tits: a response to brood size manipulation. Funct Ecol 12:750–756

Lane RA (1996) Avian hematology. In: Rosskopf W J, Woerpel RW (eds) Diseases of cage and aviary birds, 3rd edn. Williams and Wilkins, Baltimore, pp 145–158

Lanyon SM, Thompson CF (1986) Site fidelity and habitat quality as determinants of settlement patterns in male painted buntings. Condor 88:206–210

Mancke RG, Gavin TA (2000) Breeding bird density in woodlots: effects of depth and building at the edges. Ecol Appl 10: 598–611

Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886

Martin TE (1987) Food as a limit on breeding birds: a life-history perspective. Annu Rev Ecol Syst 18:453–487

Matlack GR (1993) Microenvironment variation within and among forest edge sites in the eastern United States. Biol Conserv 66:185–194

Maxwell MH (1993) Avian blood leucocyte responses to stress. World's Poult Sci J 49:34–43

Maxwell MH, Robertson GW, Anderson IA, Dick LA, Lynch M (1991) Haematology and histopathology of seven-week-old broilers after food restriction. Res Vet Sci 50:290–297

McKilligan NG (1996) Field experiments on the effect of ticks on breeding success and chick health of cattle egrets. Aust J Ecol 21:442–449

Messier F, Huot J, Goudreault F, Tremblay A (1987) Reliability of blood parameters to assess the nutritional status of caribou. Can J Zool 65:2413–2416

Moreno J, de Leon A, Fargallo JA, Moreno E (1998) Breeding time, health and immune response in the chinstrap penguin *Pygoscelis antarctica*. Oecologia 115:312–319

Morris DW (1989) Density-dependent habitat selection: testing theory with fitness data. Evol Ecol 3:80–94

Morton ML (1994) Hematocrits in montane sparrows in relation to reproductive schedule. Condor 96:119-126

Nolan V Jr (1978) The ecology and behavior of the prairie warbler *Dendroica discolor,* No 26. The Birds of North America, Philadelphia

Norušis MJ (1990) SPSS advanced statistics. SPSS, Chicago

Ots I, Hõrak P (1996) Great tits *Parus major* trade health for reproduction. Proc R Soc Lond B 263:1443–1447

Ots I, Hõrak P (1998) Health impact of blood parasites in breeding great tits. Oecologia 116:441–448

Ots I, Murumagi A, Hõrak P. 1998. Haematological health state indices of reproducing Great Tits: methodology and sources of natural variation. Funct Ecol 12:700–707

Paton PW (1994) The effect of edge on avian nest success: how strong is the evidence? Conserv Biol 8:17–26

Petit LJ, Petit DR (1996) Factors governing habitat selection by prothonotary warblers: field tests of the Fretwell-Lucas models. Ecol Monogr 66:367–387

Pyle P (1987) Identification guide to North American birds. Slate Creek, Bolinas

Rising JD, Somers KM (1989) The measurement of overall body size in birds. Auk 106:666–674

Sherry TW, Holmes RT (1996) Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. Ecology 77:36–48

Siegel HS (1985) Immunological responses as indicators of stress. World's Poult Sci J 41:36–44

Sturkie P D (1976) Avian physiology. Springer, Berlin Heidelberg New York

Ulfstrand S, Alatalo RV, Carlson A, Lundberg A (1981) Habitat distribution and body size of the Great Tit *Parus major*. Ibis 123:494–499

Wenny DG, Clawson RL, Faaborg J, Sheriff SL (1993) Population density, habitat selection and minimum area requirements of three forest-interior warblers in central Missouri. Condor 95:968–979

Wingfield JC, Hahn TP (1994) Testosterone and territorial behaviour in sedentary and migratory sparrows. Anim Behav 4:77–89

Zanette L, Doyle P, Tremont SM (2000) Food shortage in small fragments: evidence from an area-sensitive passerine. Ecology 81:1654–666

Zar JH (1996) Biostatistical analysis. Prentice-Hall, Englewood Cliffs

Zuk M (1996) Disease, endocrine-immune interactions, and sexual selection. Ecology 77:1037–1042