



**Division of Comparative Physiology and Biochemistry, Society for Integrative and Comparative Biology**

---

Does Exurban Housing Development Affect the Physiological Condition of Forest-Breeding Songbirds? A Case Study of Ovenbirds ( *Seiurus aurocapillus* ) in the Largest Protected Area in the Contiguous United States

Author(s): Chad L. Seewagen, Michale Glennon and Susan B. Smith

Source: *Physiological and Biochemical Zoology*, (-Not available-), p. 000

Published by: [The University of Chicago Press](#). Sponsored by the [Division of Comparative Physiology and Biochemistry, Society for Integrative and Comparative Biology](#)

Stable URL: <http://www.jstor.org/stable/10.1086/681025>

Accessed: 16/03/2015 12:06

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



*The University of Chicago Press and Division of Comparative Physiology and Biochemistry, Society for Integrative and Comparative Biology are collaborating with JSTOR to digitize, preserve and extend access to Physiological and Biochemical Zoology.*

<http://www.jstor.org>

# Does Exurban Housing Development Affect the Physiological Condition of Forest-Breeding Songbirds? A Case Study of Ovenbirds (*Seiurus aurocapillus*) in the Largest Protected Area in the Contiguous United States

Chad L. Seewagen<sup>1,\*</sup>

Michale Glennon<sup>2</sup>

Susan B. Smith<sup>3</sup>

<sup>1</sup>Natural Resources Department, Allee King Rosen and Fleming, 34 South Broadway, White Plains, New York 10601; and Department of Environmental Studies and Science, Pace University, 861 Bedford Road, Pleasantville, New York 10570;

<sup>2</sup>Wildlife Conservation Society, Adirondack Program, 132 Bloomingdale Avenue, Saranac Lake, New York 12983;

<sup>3</sup>Thomas H. Gosnell School of Life Sciences, Rochester Institute of Technology, 85 Lomb Memorial Drive, Rochester, New York 14623

Accepted 2/11/2015; Electronically Published 3/16/2015

## ABSTRACT

Exurban development (low-density development in rural areas) can significantly alter wildlife community composition, but it is largely unknown whether it also affects wildlife at the individual level. We investigated individual-level impacts of exurban development in New York State's Adirondack Park by comparing the physiological condition of 62 male ovenbirds (*Seiurus aurocapillus*) breeding in forests with low-density housing development with those in contiguous forests. We used hematocrit (HCT) volume and plasma triglyceride (TRIG) levels to compare energetic condition, plasma uric acid (UA) and total plasma protein (TPP) levels to compare diet quality, and heterophil:lymphocyte ratios (H:L) to compare chronic stress. HCT was the only parameter to differ, with birds near houses exhibiting lower values. The comparable TRIG, UA, and TPP that we found between treatment types suggest that ovenbird food quality and availability are unaffected by exurban development in our study area. Similar H:L suggests that homeowner activities do not significantly change chronic stressors faced by breeding male ovenbirds. We also found no difference in body mass, body size, or age ratio to indicate that habitats in either treatment type were in higher demand or

more difficult to acquire. Although our results suggest that exurban development does not reduce habitat quality for male ovenbirds in a way that affects their condition, we caution that it may still ultimately reduce fitness by attracting synanthropic predators. Further work is needed to better understand the impacts of exurban development on wildlife at all levels and provide science-based information needed to meet conservation challenges in rapidly developing exurban areas.

**Keywords:** conservation physiology, development in protected areas, housing development, condition index, Adirondack Park.

## Introduction

Low-density residential development in rural areas—or exurbanization—is the most common and fastest growing form of land use change in the United States today, proceeding at several times the pace of urbanization and suburbanization combined and occupying nearly 15 times the total land area (Brown et al. 2005). Moreover, exurban development is often disproportionately concentrated within or around protected lands and other areas of high conservation importance (Wade and Theobald 2009; Radeloff et al. 2010). Unlike many other land uses, exurban development leaves most of the surrounding landscape physically unchanged, giving the perception that its effects on biodiversity are minimal (Maestas et al. 2001). In actuality, however, there is mounting evidence linking exurbanization to significant alterations in wildlife community composition and biotic integrity (e.g., Glennon and Porter 2005; Glennon and Kretser 2013; Wood et al. 2014).

Exurban homes occupy several acres at the parcel level, resulting in a considerably greater per capita spatial footprint than the higher-density residential development of urban and suburban areas. Another important difference between exurbanization and these other forms of development is that the former leaves the surrounding matrix in its original ecosystem type (Maestas et al. 2001; Odell and Knight 2001). In exurbia, houses are imbedded at low densities within an otherwise largely intact, contiguous forest or other habitat type; the reverse occurs in suburbia and cities, where habitat islands are often isolated within a matrix of development, having lost many of the properties of the original system. As such, it is

\*Corresponding author; e-mail: cseewagen@pace.edu.

uncertain to what extent the well-documented impacts to birds and other wildlife from habitat loss and fragmentation associated with suburban and urban development can be generalized to exurbia.

Most studies of the effects of exurbanization on wildlife have examined patterns in diversity, abundance, and community composition (e.g., Glennon and Porter 2005; Suarez-Rubio et al. 2011, 2013; Glennon and Kretser 2013; Lumpkin and Pearson 2013). Although it is important to understand how exurban development alters these properties of surrounding biological communities, such metrics provide poor information about habitat quality, and they fail to indicate how the fitness of individuals and their populations are affected (Van Horn 1983; Bock and Jones 2004; Johnson 2007). This is particularly so in human-modified environments, where maladaptive habitat selection and ecological traps are common (Schlaepfer et al. 2002; Battin et al. 2004; Robertson and Hutto 2006). A comprehensive evaluation of the response of wildlife to environmental change is best achieved by considering all three primary levels of biological organization: community, population, and individual (e.g., Frankel 2001; Pidgeon et al. 2006).

The goal of our study was to investigate potential individual-level impacts of exurban development to wildlife by comparing the physiological condition of a forest songbird, the ovenbird (*Seiurus aurocapilla*), breeding in areas of the Adirondack Mountains, New York, with and without exurban housing development. An animal's physiological condition is critical to its fitness and survival and can provide sensitive signals of change in habitat quality (Wikelski and Cooke 2006; Cooke et al. 2013). Exurban homes in the Adirondacks have been shown to cause significant shifts in bird community structure, usually with generalist and edge species increasing in abundance at the expense of more sensitive, forest interior species (Glennon and Kretser 2013; Glennon et al. 2014). Similar responses of bird communities to exurban housing development have been observed in California (Merenlender et al. 2009), Montana (Glennon et al. 2014), New England (Kluza et al. 2000), the mid-Atlantic (Suarez-Rubio et al. 2013), and elsewhere across the United States (Wood et al. 2014). However, while many species are displaced by the construction of a new home, some species that are typically considered to be sensitive to forest fragmentation and anthropogenic disturbance—such as our model organism, the ovenbird (Porneluzi et al. 2011)—will often remain in the wake of the development and continue to inhabit the area (Kluza et al. 2000; Glennon and Kretser 2013). Despite their continued presence within forest habitats surrounding exurban homes, these species may still experience adverse impacts to their condition, reproductive success, or survival that would go undetected by studies of community-level variables.

We compared five common physiological condition indices in male ovenbirds breeding in areas of the Adirondacks with low-density housing development with those inhabiting large tracts of contiguous forest nearby in order to investigate the impacts of exurbanization on forest wildlife at the individual level. Specifically, we used hematocrit (HCT) volume and

plasma triglyceride (TRIG) levels to assess energetic condition (Mazerolle and Hobson 2002b; Masello and Quillfeldt 2004; Kilgas et al. 2006), plasma uric acid (UA) and total plasma protein (TPP) levels to assess diet quality (i.e., dietary protein content; Brown 1996; Smith et al. 2007), and heterophil to lymphocyte ratios (H:L) to measure chronic stress (Ruiz et al. 2002; Suorsa et al. 2004; Owen et al. 2005; Davis et al. 2008). If woodlands surrounding exurban homes provide poorer-quality habitat and present more physiologically demanding conditions than intact forest, birds breeding near houses would be expected to exhibit lower levels of HCT, TRIG, UA, and TPP and higher H:L ratios.

## Material and Methods

### Study Area

New York State's Adirondack Park is approximately 25,000 km<sup>2</sup> and is the largest protected area in the contiguous United States (Jenkins and Keal 2004). The topography is mountainous (elevations range approximately 400–1,200 m), and the dominant land cover types are northern hardwood, mixed hardwood-conifer, and boreal forests. The Adirondack Park is uniquely composed of a mixture of public and private land, with nearly 60% of the park privately owned and hosting more than 135,000 full-time residents and 250,000 second-home owners. Hundreds of new houses are approved for development in the park each year (Jenkins and Keal 2004). This rapid, low-density residential growth makes the Adirondack region an ideal system in which to examine the biological impacts of exurban development.

Our study sites for both treatment types (i.e., houses and reference forests with no houses) were in the northeastern region of the Adirondack Park in the municipalities of Keene, Keene Valley, Lake Placid, and Saranac Lake (Essex County). We captured ovenbirds opportunistically at a subset of the houses currently included in an ongoing, separate study of the ecological and sociological mechanisms underlying the effects of exurban development on bird and mammal community composition in the Adirondack Park (National Science Foundation BSC-1060505; also see Glennon et al. 2014). These houses were originally selected on the basis of having lot sizes of 2–40 acres (a common definition of exurban [Theobald 2001, 2005]), appropriate surrounding habitat for the study species (mature hardwood or mixed forest), landowner permission to access the property, and the presence of potential reference areas nearby. The houses around which we captured ovenbirds are located within five areas zoned for low-density residential subdivision, and we treated each house as an independent unit because of the large degree of variation in parcel size, house size, lawn size (and other measures of landscaping intensity), levels of human activity (e.g., full-time vs. part-time residents), and other characteristics among properties. For comparison to ovenbirds nesting near houses, we captured ovenbirds at six reference areas also used by Glennon and Kretser (2013) and Glennon et al. (2014) that are undeveloped, have low levels of human activity, and are protected as New

York State Forest Preserve lands. Reference areas were chosen by identifying the closest areas of accessible undeveloped land of the same habitat type as the housing sites and of sufficient size to contain interior forest far from houses and roads. The longest distance between any houses or reference areas is 36.2 km, while the shortest is 1.5 km (one a housing site and the other a reference area in both cases). Sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*)—and, to a lesser extent, birches (*Betula* spp.)—are dominant trees among our housing and reference areas, and tree density, size, and canopy cover are also similar (M. Glennon, unpublished data). The primary difference between the two treatment types is therefore the presence or absence of houses and their associated infrastructure (e.g., access roads, driveways, utility lines).

At sites with houses, we attempted to capture only ovenbirds that were heard singing within an estimated 200 m, on the basis of the findings of Glennon and Kretser (2013) that the influence of exurban homes on bird community composition in the Adirondack Park extends up to 200 m from the edge of the lawn into the surrounding forest. Likewise, we attempted to capture only birds at reference sites that were heard singing well beyond 200 m from any house or road. Global positioning system coordinates were recorded in the field for each capture location, and distances to nearest houses and roads were subsequently measured using Google Maps.

#### *Bird Capture and Blood Sampling*

All birds used in the study were captured between 0600 and 1230 hours Eastern Standard Time, June 6–16 (the peak period of active nesting for ovenbirds in the area), 2012 and 2013, using a playback recording and mist net set up in the vicinity of a singing male. Up to 150  $\mu$ L of blood was collected by brachial venipuncture with a 26-gauge needle into heparinized capillary tubes immediately following capture. An additional bead of blood was then used to prepare a smear on a microscope slide for measurement of H:L (during 2013 only). After collecting blood, we banded each bird with a U.S. Geological Survey aluminum leg band and measured unflattened wing length (to 1 mm) and body mass (to 0.1 g on a digital balance). Birds were aged as second year or after second year on the basis of plumage (Pyle 1997) and then released. Bird capture and blood sampling was authorized by the U.S. Department of the Interior (banding permit 23755) and the New York State Department of Environmental Conservation (license to collect and possess banding 114).

Capillary tubes were centrifuged for 10 min, and smears were fixed in absolute ethanol and stained using the Protocol Hema 3 Stat Pack (Fisher Scientific, Kalamazoo, MI) at the end of each day. HCT volume was measured in the centrifuged capillary tubes with digital calipers to 0.1 mm and expressed as the proportion of whole blood volume. The plasma was transferred to 0.6-mL cryogenic tubes and stored at  $-20^{\circ}\text{C}$  for up to 2 wk until the end of the field season. Plasma samples were then overnight shipped to the Rochester Institute of Technology (Rochester, NY) and stored at  $-80^{\circ}\text{C}$  for up to 6 mo until analysis.

#### *Condition Indices*

HCT, the proportion of packed red cells to whole blood volume, is a widely reported hematological indicator of overall health in field studies of birds (Brown 1996; Fair et al. 2007; Garvin et al. 2008; Milenkaya et al. 2013), likely in part because of the simplicity of its measurement. Generally, HCT increases with oxygen carrying capacity and decreases with infection intensity, malnutrition, and starvation. However, HCT may also rise as a result of dehydration, and the aforementioned patterns are not always consistent, making HCT difficult to interpret and often discounted as a reliable condition index (Dawson and Bortolotti 1997; Cuervo et al. 2007; Fair et al. 2007; Lill et al. 2013). Use of HCT as a sole indicator of condition is not recommended (Fair et al. 2007). TRIG reflects the rate of absorption and transport of dietary or de novo synthesized lipids through the bloodstream to adipose tissue and is thereby representative of a bird's recent feeding activity and energetic condition. TRIG is elevated in birds that are in a state of positive energy balance, whereas TRIG is depressed in birds that are underfed and losing body mass (Jenni-Eiermann and Jenni 1994; Cerasale and Guglielmo 2006). TPP (the total amount of globulin, albumin, and other proteins in avian blood plasma) increases in relation to dietary protein content (Levielle and Sauberlich 1961) and is therefore commonly used as an indicator of diet quality and nutritional status (Gavett and Weakley 1986; Brown 1996; Mazerolle and Hobson 2002b; Schoech and Bowman 2003; Milenkaya et al. 2013). We also assessed diet quality by measuring UA, a blood plasma metabolite that also increases along with dietary protein content (Machín et al. 2004; Smith et al. 2007). Heterophils and lymphocytes are white blood cells that increase and decrease, respectively, in response to immune challenges and in concert with elevated corticosterone levels. Their ratio, H:L, is therefore considered indicative of infection and chronic stress in birds (Ruiz et al. 2002; Suorsa et al. 2004; Owen et al. 2005; Davis et al. 2008). In addition to these hematological parameters, we also used body mass—adjusted to body size (wing length) with a scaled mass model (Peig and Green 2009)—to compare the condition of ovenbirds between both treatment types.

#### *Laboratory Analyses*

Plasma samples were diluted threefold with 0.9% saline before all analyses to increase sample volume (Guglielmo et al. 2005; Smith and McWilliams 2010). In cases where sample volumes were still too small to complete all analyses, priority was given to TRIG, followed by UA and then TPP. TRIG was measured using a sequential endpoint microplate assay (Sigma Aldrich), as described by Guglielmo et al. (2005), and UA was measured by colorimetric endpoint microplate assay (TECO Diagnostics), as described by Smith and McWilliams (2010). We measured TPP with a Biuret colorimetric endpoint microplate assay (Sigma Total Protein Reagent T1949; Krohn 2001). A chicken plasma pool was run on each microplate to assess inter-assay

variation for all assays. All samples and standards were run in duplicate wells, and sample measurements were repeated until the coefficient of variation between two replicate wells was <10%. We used a compound light microscope at  $\times 1,000$  magnification under oil immersion to examine the blood smears and calculate the ratio of heterophils to lymphocytes out of 100 total randomly selected leukocytes (Campbell 1995). All counts were performed by the same observer.

### Statistical Analyses

We used general linear models with a backward selection procedure ( $\alpha = 0.1$ ) to explore variables besides treatment type that may also contribute to variation in the physiological condition indices. The additional variables examined included capture time, time elapsed between capture and blood sample collection (bleed time; excepting H:L because of no biological reason to expect an effect), age (second year, after second year), size-adjusted body mass, and year. We then explicitly compared the physiological condition indices between treatment types using ANCOVA, with variables retained by the general linear models entered as the covariates (Guglielmo et al. 2005; Seewagen et al. 2011). All covariates met assumptions of equal variance and homogeneous slopes.

Wing length and size-adjusted body mass were compared between treatment types with *t*-tests, with data from 2012 and 2013 pooled after confirming there were no differences between years. Age ratios were compared using Fisher's exact test. We ran statistical analyses using SAS and SYSTAT and interpreted results as significant when  $P < 0.05$ , with the exception of the backward selection procedure, where variables were retained when  $P < 0.1$ . UA and H:L data were log transformed, and HCT data were logit transformed before analyses to meet normality assumptions.

### Results

We obtained blood samples from a total of 31 birds near houses and 31 birds from the reference sites (17 birds per treatment type during 2012 and 14 birds per treatment type during 2013).

Final sample sizes for each condition index varied slightly (table 1). Birds at sites with exurban development were captured an average of 86 m (range = 13–165 m) from the closest house. At the reference sites, birds were captured an average of 826 m (range = 351–2,000 m) from the closest house (and an average of 875 m [range = 352–2,400 m] from the closest road), well beyond the maximum home range sizes observed in breeding ovenbirds (Porneluzi et al. 2011).

Variables retained by the backward selection procedure and included as covariates in the ANCOVAs varied among the condition indices, although neither size-adjusted body mass nor age was retained for any condition index, and bleed time accounted for significant variation in three of the condition indices, despite bleed times being generally short (mean  $\pm$  SD =  $9 \pm 2$  min). TRIG was positively related to capture time ( $P < 0.001$ ) and negatively related to bleed time ( $P = 0.08$ ) and year ( $P = 0.06$ ). UA and TPP were negatively related to bleed time ( $P = 0.003$  and  $0.04$ , respectively), H:L was positively related to capture time ( $P = 0.07$ ), and HCT was negatively related to year ( $P < 0.001$ ).

TRIG did not differ between houses and the reference sites when the effects of bleed time, capture time, and year were controlled for ( $F_{4,57} = 0.09$ ,  $P = 0.77$ ; fig. 1). There was also no difference between treatment types in UA ( $F_{2,58} = 0.21$ ,  $P = 0.65$ ) or TPP ( $F_{2,53} = 0.01$ ,  $P = 0.91$ ) when the effect of bleed time was held constant or H:L when the effect of capture time was held constant ( $F_{2,24} = 0.01$ ,  $P = 0.76$ ; fig. 1). After controlling for the effect of year, HCT was the only hematological condition index to differ between houses and the reference sites, with birds at the reference sites averaging higher HCT volumes ( $F_{2,57} = 5.65$ ,  $P = 0.021$ ; fig. 1). Ovenbirds near houses and within reference sites did not differ in wing length ( $t_{1,60} = 1.17$ ,  $P = 0.25$ ) or size-adjusted body mass ( $t_{1,60} = 0.59$ ,  $P = 0.56$ ). Age ratio also did not differ between treatment types ( $P = 0.80$ ).

### Discussion

Exurban development has been shown to cause significant changes in the abundance and community composition of

Table 1: Age ratios and mean ( $\pm$  SE) wing length, body mass, and physiological condition indices of breeding male ovenbirds in Adirondack Park, New York, 2012–2013

Parameter	Houses	Reference forests
Age ratio (second year/after second year)	14/17	15/16
Wing length (mm)	76 $\pm$ .4 (31)	76 $\pm$ .3 (31)
Body mass (g)	19.4 $\pm$ .2 (31)	19.6 $\pm$ .2 (31)
Hematocrit volume	.49 $\pm$ .03 (30)	.52 $\pm$ .06 (30)
Plasma triglyceride (mmol)	.98 $\pm$ .38 (31)	.98 $\pm$ .26 (31)
Plasma uric acid (mmol)	1.09 $\pm$ .35 (31)	1.07 $\pm$ .31 (30)
Total plasma protein (mg/mL)	32.40 $\pm$ 4.77 (29)	32.83 $\pm$ 6.37 (27)
Heterophil:lymphocyte	.65 $\pm$ .35 (14)	.63 $\pm$ .42 (13)

Note. Sample sizes are shown in parentheses.

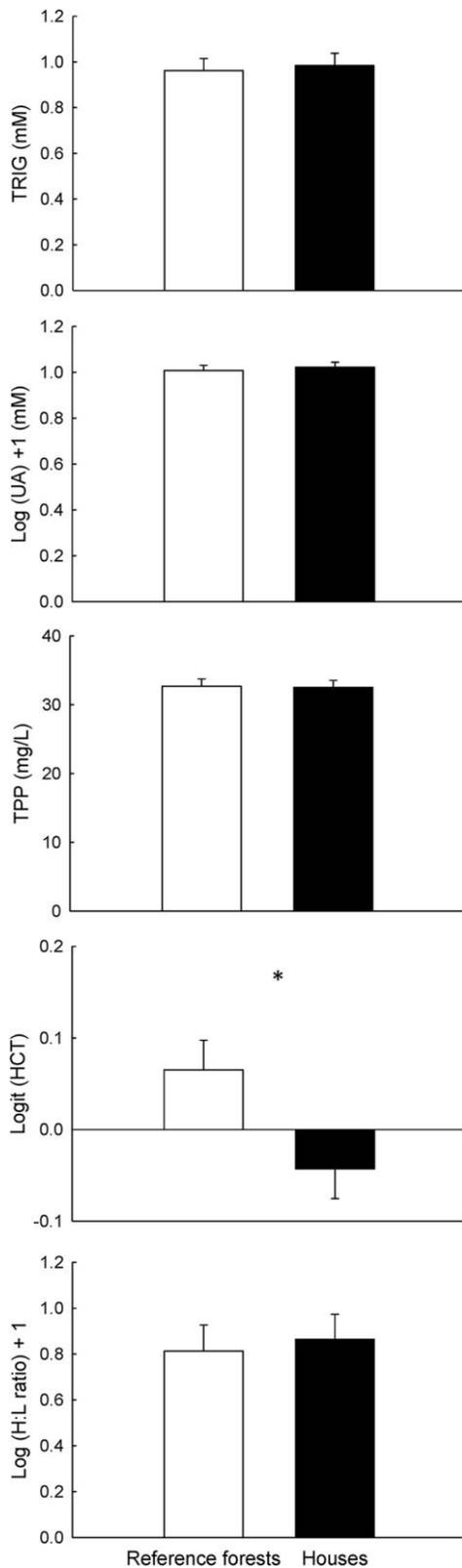


Figure 1. Least squares mean (+SE) hematocrit (HCT) volumes, plasma triglyceride (TRIG) levels, plasma uric acid (UA) levels, total plasma protein (TPP) levels, and heterophil to lymphocyte ratios (H:L) of male ovenbirds breeding near exurban houses and in

birds and other wildlife, but few studies have investigated physiological effects, despite their potentially strong influences on survival and population viability and their utility for identifying responses of wildlife to anthropogenic disturbances (Wikelski and Cooke 2006; Busch and Hayward 2009). Here, we found no evidence to suggest that exurban development in New York's Adirondack Park reduces habitat quality for male ovenbirds in a way that affects their physiological condition. HCT, the least informative and reliable of our five physiological condition indices, was the only one to differ between ovenbirds with nesting territories near houses and those holding territories in large tracts of contiguous forest. Possibly ectoparasites accounted for the difference in HCT between groups (Heylen and Matthysen 2008), but no birds approached anemic HCT volumes (<35%; Campbell and Ellis 2007) that would indicate significant parasitism, disease, or nutritional stress, and we do not consider the difference in HCT between groups to be reliably indicative of any differences in habitat quality (Dawson and Bortolotti 1997; Fair et al. 2007). We also found no difference in age ratio or body size to suggest that habitats in either treatment type were in higher demand or more difficult to acquire and defend.

The ovenbird has commonly been used as a model organism to study the effects of forest fragmentation from various sources, including roads (Ortega and Capen 1999), logging (King et al. 1996; Gram et al. 2003), energy development (Bayne et al. 2005a, 2005b; Machtans 2006), agriculture (Bayne and Hobson 2001; Mazerolle and Hobson 2002b), and urban sprawl (Mancke and Gavin 2000; Frankel 2001; Morimoto et al. 2012). Responses of ovenbirds to these forms of disturbance have varied, and geographic differences in their area requirements are apparent, but in general, forest fragmentation has been observed to negatively affect ovenbird abundance, pairing success, nest success, fledging success, and overall productivity (reviewed in Porneluzi et al. 2011). In an individual-level study similar to ours, however, Mazerolle and Hobson (2002b) found that male ovenbirds breeding in contiguous forest in Saskatchewan, Canada, actually had poorer hematological indicators of energetic condition and chronic stress than those breeding in small forests fragmented by agriculture. The authors reasoned that territory defense in the contiguous forest—where reproductive success and densities of breeding pairs were known to be higher (Bayne and Hobson 2001)—came at a greater physiological cost than holding territories in small forest fragments that were suboptimal (also see Mazerolle and Hobson 2004). Relative abundance estimates (corrected for detection probability) from bird point counts that were performed at our study sites and additional, similar sites for a separate study did not differ between houses and reference areas (M. Glennon, unpublished data), suggesting that ovenbird density is likely comparable between our treatment types. Mazerolle and Hobson (2002b) found that the ovenbirds in the contiguous forest were also

reference forests in Adirondack Park, New York, 2012–2013. Asterisk indicates statistical significance (ANCOVA:  $F_{2,57} = 5.65$ ,  $P = 0.021$ ).

significantly larger, possibly indicating that territories in contiguous forest were in greater demand and acquired by the largest, most dominant individuals. It is important to recognize that an animal's condition may be either a consequence or a determinant of habitat acquisition. We found nothing to suggest that a territorial male ovenbird's condition either determined or resulted from its selection of breeding habitat near houses or in large forested tracts lacking exurban residential development. Body size was not consistently different between treatment types, and in contrast to Bayne and Hobson's (2002) study within an agricultural landscape, we did not find that occupation of contiguous forests was skewed toward adult ovenbirds while first-time breeders (second-year birds) acquired territories mostly in fragmented forest. The degree of forest fragmentation from exurban housing development is extremely minor compared with that caused by agriculture and most other forms of land use change (Maestas et al. 2001; Odell and Knight 2001) and appears to be minimal enough to not affect habitat quality for male ovenbirds in a way that affects their condition.

Mechanisms underlying community-level effects of exurban development on birds in the Adirondacks and elsewhere remain unclear, but as with urban, suburban, and agricultural development, physical alteration of the habitat could be the primary driver. Alternatively, it has been proposed that the presence and behavior of the homeowners (e.g., motor vehicles, outdoor pets, landscaping activities, artificial lighting, and other introduced human disturbances) may be more important than the land development per se (Hansen et al. 2005; Schlesinger et al. 2008). In any case, we would expect these same factors to affect the physiological condition of birds in addition to their community composition by changing food availability (Burke and Nol 1998), noise levels (Habib et al. 2007), perceived predation risk (Zanette et al. 2011; Newman et al. 2013), or other important habitat characteristics. Stress levels of forest birds, for example, have been shown to be increased by both fragmentation (Suorsa et al. 2003; Leshyk et al. 2012; Dantzer et al. 2014; but see Suorsa et al. 2004) and human disturbance (Dietz et al. 2013; Dantzer et al. 2014), yet the ovenbirds we studied did not exhibit different H:L between nesting territories near houses or in intact forest. This suggests that homeowner activities do not significantly change chronic stressors faced by breeding male ovenbirds, although H:L may not always respond to all forms of chronic stress (Müller et al. 2011). Forest fragmentation is sometimes found to reduce arthropod prey biomass for ovenbirds and other songbirds (Burke and Nol 1998; Zanette et al. 2000) but not always (Buehler et al. 2002; Mazerolle and Hobson 2002a). The comparable levels of TRIG, UA, and TPP that we found between ovenbirds in areas with and without houses suggest that both the availability and the quality of food for ovenbirds is unaffected by exurban development in our study area. Consistent with this finding, Casey et al. (2009) found the abundance of ground-dwelling arthropods (the primary food source of ovenbirds) to be unaffected by exurban development in forests of Tennessee. We cannot eliminate the possibility, however, that the male ovenbirds in our study adjusted their provisioning effort to

maintain their own condition at the expense of their mate and nestlings.

Although our results indicate that the physical condition and health of breeding male ovenbirds is not affected by exurban development, exurban development may cause other individual- or population-level impacts through lowered reproductive success and survival by attracting and creating favorable conditions for synanthropic species that are common predators of small passerines at the egg, nestling, fledgling, and/or adult stage (e.g., domestic cat [*Felis catus*], blue jay [*Cyanocitta cristata*], American crow [*Corvus brachyrhynchos*]). Indeed, exurban development has been found to result in increased nest predation rates among forest-breeding songbirds in Virginia (Lumpkin and Pearson 2013) and Ontario (Phillips et al. 2005). An investigation into nest predation rates and overall nest success in our study sites is currently ongoing. We also caution that it is possible that female and nestling ovenbirds—as well as other species in our study system and elsewhere—are more sensitive to exurban development and experience impacts to their condition and health while adult male ovenbirds do not. Further research is needed to better understand the impacts (and underlying mechanisms) of exurban development on wildlife at all levels and ultimately provide conservation practitioners, resource managers, and policymakers with the science-based information needed to meet conservation challenges in the face of rising development pressures in exurban areas.

#### Acknowledgments

Field work was funded by grants to C.L.S. from Northern New York Audubon, and laboratory work was funded through support from the Gosnell School of Life Sciences and the College of Science at Rochester Institute of Technology for Faculty Development Funding to S.B.S. We also thank S. Sphalski, D. Reinhardt, and C. Gould for assistance with laboratory analyses and S. van Laer and H. Imran-Khan for help in the field.

#### Literature Cited

- Battin J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conserv Biol* 18:1482–1491.
- Bayne E.M., S. Boutin, B. Tracz, and K. Charest. 2005a. Functional and numerical responses of ovenbirds (*Seiurus aurocapilla*) to changing seismic exploration practices in Alberta's boreal forest. *Ecoscience* 12:216–222.
- 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.
- . 2002. Apparent survival of male ovenbirds in fragmented and forested boreal landscapes. *Ecology* 83:1307–1316.
- Bayne E.M., S.L. Van Wilgenburg, S. Boutin, and K.A. Hobson. 2005b. Modeling and field testing of ovenbird

- (*Seiurus aurocapillus*) responses to boreal forest dissection by energy sector development at multiple spatial scales. *Landsc Ecol* 20:203–216.
- Bock C.E. and Z.F. Jones. 2004. Avian habitat evaluation: should counting birds count? *Front Ecol Environ* 2:403–410.
- Brown D.G., K.M. Johnson, T.R. Loveland, and D.M. Theobald. 2005. Rural land use trends in the conterminous United States, 1950–2000. *Ecol Appl* 15:1851–1863.
- Brown M.E. 1996. Assessing body condition in birds. *Curr Ornithol* 13:67–135.
- Buehler D.M., D. Norris, B.J.M. Stutchbury, and N.C. Kopysh. 2002. Food supply and parental feeding rates of hooded warblers in forest fragments. *Wilson Bull* 114:122–127.
- Burke D.M. and E. Nol. 1998. Effects of food abundance, nest site habitat, and forest fragmentation on breeding ovenbirds. *Auk* 115:96–104.
- Busch D.S. and L.S. Hayward. 2009. Stress in a conservation context: a discussion of glucocorticoid actions and how levels change with conservation-relevant variables. *Biol Conserv* 142:2844–2853.
- Campbell T.W. 1995. Avian hematology and cytology. Blackwell, Ames, IA.
- Campbell T.W. and C.K. Ellis. 2007. Avian and exotic animal hematology and cytology. Blackwell, Ames, IA.
- Casey J.M., M.E. Wilson, N. Hollingshead, and D.G. Haskell. 2009. The effects of exurbanization on bird and macroinvertebrate communities in deciduous forests on the Cumberland Plateau, Tennessee. *Int J Ecol* 2009:539417.
- Cerasale D.J. and C.G. Guglielmo. 2006. Dietary effects on prediction of body mass changes in birds by plasma metabolites. *Auk* 123:836–846.
- Cooke S.J., L. Sack, C.E. Franklin, A.P. Farrell, J. Beardall, M. Wikelski, and S.L. Chown. 2013. What is conservation physiology? perspectives on an increasingly integrated and essential science. *Conserv Physiol* 1:cot001. doi:10.1093/conphys/cot001.
- Cuervo J.J., A.P. Moller, and F. De Lope. 2007. Haematocrit is weakly related to condition in nestling barn swallows *Hirundo rustica*. *Ibis* 149:128–134.
- Dantzer B., Q.E. Fletcher, R. Boonstra, and M.J. Sheriff. 2014. Measures of physiological stress: a transparent or opaque window into the status, management and conservation of species? *Conserv Physiol* 2:cou023. doi:10.1093/conphys/cou023.
- Davis A.K., D.L. Maney, and J.C. Maerz. 2008. The use of leukocyte profiles to measure stress in vertebrates: a review for ecologists. *Funct Ecol* 22:760–772.
- Dawson R.D. and G.R. Bortolotti. 1997. Are avian hematocrits indicative of condition? American kestrels as a model. *J Wildl Manage* 61:1297–1306.
- Dietz M.S., C.C. Murdock, L.M. Romero, A. Ozgul, and J. Foufopoulos. 2013. Distance to a road is associated with reproductive success and physiological stress response in a migratory landbird. *Wilson J Ornithol* 125:50–61.
- Fair J., S. Whitaker, and B. Pearson. 2007. Sources of variation in haematocrit in birds. *Ibis* 149:535–552.
- Frankel M.A. 2001. Avian community, population, and behavioral patterns in a forested, suburban landscape. PhD diss. Boston University.
- Garvin J.C., P.O. Dunn, L.A. Whittingham, D.A. Steeber, and D. Hasselquist. 2008. Do male ornaments signal immunity in the common yellowthroat? *Behav Ecol* 19:54–60.
- Gavett A.P. and J.S. Wakeley. 1986. Blood constituents and their relation to diet in urban and rural house sparrows. *Condor* 88:279–284.
- Glennon M.J. and H. Kretser. 2013. Size of the ecological effect zone associated with exurban development in the Adirondack Park. *Landsc Urban Plann* 112:10–17.
- Glennon M.J., H.E. Kretser, and J.A. Hilty. 2014. Identifying common patterns in diverse systems: effects of exurban development on birds of the Adirondack Park and the Greater Yellowstone Ecosystem, USA. *Environ Manage* 55:453–466. doi:10.1007/s00267-014-0405-9.
- Glennon M.J. and W.F. Porter. 2005. Effects of land use management on biotic integrity: an investigation of bird communities. *Biol Conserv* 126:499–511.
- Gram W.K., P.A. Porneluzi, R.L. Clawson, J. Faaborg, and S.C. Richter. 2003. Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark Forests. *Conserv Biol* 17:1324–1337.
- Guglielmo C.G., D.J. Cerasale, and C. Eldermire. 2005. A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. *Physiol Biochem Zool* 78:116–125.
- Habib L., E.M. Bayne, and S. Boutin. 2007. Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. *J Appl Ecol* 44:176–184.
- Hansen A.J., R. Knight, J. Marzluff, S. Powell, K. Brown, P. Gude, and K. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecol Appl* 15:1893–1905.
- Heylen D.J.A. and E. Matthysen. 2008. Effect of tick parasitism on the health status of a passerine bird. *Funct Ecol* 22:1099–1107.
- Jenkins J. and A. Keal. 2004. The Adirondack atlas: a geographic portrait of the Adirondack Park. Syracuse University Press, Syracuse, NY.
- Jenni-Eiermann S. and L. Jenni. 1994. Plasma metabolite levels predict individual body-mass changes in a small long-distance migrant, the garden warbler. *Auk* 111:888–899.
- Johnson M.D. 2007. Measuring habitat quality: a review. *Condor* 109:489–504.
- Kilgas P., R. Mand, M. Magi, and V. Tilgar. 2006. Hematological parameters in brood rearing great tits in relation to habitat, multiple breeding and sex. *Comp Biochem Physiol A* 144:224–231.
- King D.I., C.R. Griffin, and R.M. Degraaf. 1996. Effects of clearcutting on habitat use and reproductive success of the ovenbird in forested landscapes. *Conserv Biol* 10:1380–1386.
- Kluza D.A., C.R. Griffin, and R.M. DeGraaf. 2000. Housing developments in rural New England: effects on forest birds. *Anim Conserv* 3:15–26.

- Krohn R. I. 2001. The colorimetric determination of total protein. *Curr Protoc Food Anal Chem B* 1:1–1.
- Leinwand I.I.F., D.M. Theobald, J. Mitchell, and R.L. Knight. 2010. Landscape dynamics at the public-private interface: a case study in Colorado. *Landsc Urban Plann* 97:182–193.
- Leshyk R., E. Nol, D.M. Burke, and G. Burness. 2012. Logging affects fledgling sex ratios and baseline corticosterone in a forest songbird. *PLoS ONE* 7:e33124. doi:10.1371/journal.pone.0033124.
- Levielle G. and H. Sauberlich. 1961. Influence of dietary protein level on serum protein components and cholesterol in the growing chick. *J Nutr* 74:500–504.
- Lill A., K. Rajchl, L. Yachou-Wos, and C.P. Johnstone. 2013. Are haematocrit and haemoglobin concentration reliable body condition indicators in nestlings: the welcome swallow as a case study. *Avian Biol Res* 6:57–66.
- Lumpkin H.A. and S.M. Pearson. 2013. Effects of exurban development and temperature on bird species in the southern Appalachians. *Conserv Biol* 27:1069–1078.
- Machín M., M. F. Simoyi, K. P. Blemings, and H. Klandorf. 2004. Increased dietary protein elevates plasma uric acid and is associated with decreased oxidative stress in rapidly-growing broilers. *Comp Biochem Physiol B* 137:383–390.
- Machtans C.S. 2006. Songbird response to seismic lines in the western boreal forest: a manipulative experiment. *Can J Zool* 84:1421–1430.
- Maestas J.D., R.L. Knight, and W.C. Gilgert. 2001. Biodiversity and land use change in the American mountain west. *Geogr Rev* 91:509–524.
- Mancke R.G. and T.A. Gavin. 2000. Bird density in woodlots: effects of depth and buildings at the edges. *Ecol Appl* 10: 598–611.
- Masello J.F. and P. Quillfeldt. 2004. Are hematological parameters related to body condition, ornamentation and breeding success in wild burrowing parrots *Cyanoliseus patagonus*? *J Avian Biol* 35:445–454.
- Mazerolle D.F. and K. A. Hobson. 2002a. Consequences of forest fragmentation on territory quality of male ovenbirds breeding in western boreal forests. *Can J Zool* 80:1841–1848.
- . 2002b. Physiological ramifications of habitat selection in territorial male ovenbirds: consequences of landscape fragmentation. *Oecologia* 130:356–363.
- Mazerolle D.F. and K.A. Hobson. 2004. Territory size and overlap in male ovenbirds: contrasting a fragmented and contiguous boreal forest. *Can J Zool* 82:1774–1781.
- Merenlender A.M., S.E. Reed, and K.L. Heise. 2009. Exurban development influences woodland bird composition. *Landsc Urban Plann* 92:255–263.
- Milenkaya O., N. Weinstein, S. Legge, and J.R. Walters. 2013. Variation in body condition indices of crimson finches by sex, breeding stage, age, time of day, and year. *Conserv Physiol* 1:cot020. doi:10.1093/conphys/cot020.
- Morimoto D.C., M.A. Frankel, M. Hersek, and F.E. Wasserman. 2012. Forest fragmentation effects on ovenbird populations in the urban region of eastern Massachusetts, USA. *Urban Habitats* 7, [http://www.urbanhabitats.org/v07n01/forestfragmentation\\_full.html](http://www.urbanhabitats.org/v07n01/forestfragmentation_full.html).
- Müller C., S. Jenni-Eiermann, and L. Jenni. 2011. Heterophils/lymphocytes-ratio and circulating corticosterone do not indicate the same stress imposed on Eurasian kestrel nestlings. *Funct Ecol* 25:566–576.
- Newman A.E.M., L.Y. Zanette, M. Clinchy, N. Goodenough, and K.K. Soma. 2013. Stress in the wild: chronic predator pressure and acute restraint affect plasma DHEA and corticosterone levels in a songbird. *Stress* 16:363–367.
- Odell E.A. and R.L. Knight. 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. *Conserv Biol* 15:1143–1150.
- 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.
- Owen J.C., M.K. Sogge, and M.D. Kern. 2005. Habitat and sex differences in physiological condition of breeding southwestern willow flycatchers (*Empidonax traillii extimus*). *Auk* 122:1261–1270.
- Peig J. and A. J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled index as an alternative method. *Oikos* 118:1883–1891.
- Phillips J., E. Nol, D. Burke, and W. Dunford. 2005. Impacts of housing developments on wood thrush nesting success in hardwood forest fragments. *Condor* 107:97–106.
- Pidgeon A.M., V.C. Radeloff, and N.E. Matthews. 2006. Contrasting measures of fitness to classify habitat quality for the black-throated sparrow (*Amphispiza bilineata*). *Biol Conserv* 132:199–210.
- Porneluzi P., M.A. Van Horn, and T.M. Donovan. 2011. Ovenbird (*Seiurus aurocapilla*). In A. Poole, ed. *The Birds of North America Online*. Cornell Lab of Ornithology, Ithaca, NY. <http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/088>.
- Pyle P. 1997. Identification guide to North American birds. Pt 1. Slate Creek, Bolinas, CA.
- Radeloff V.C., S.I. Stewart, T.J. Hawbaker, U. Gimmi, A.M. Pidgeon, C.H. Flather, R.B. Hammer, and D.P. Helmers. 2010. Housing growth in and near United States protected areas limits their conservation value. *Proc Natl Acad Sci USA* 107:940–945.
- Robertson B.A. and R.L. Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87:1075–1085.
- Ruiz G., M. Rosenmann, F. Fernando Novoa, and P. Sabat. 2002. Hematological parameters and stress index in rufous-collared sparrows dwelling in urban environments. *Condor* 104:162–166.
- Schlaepfer M.A., M.C. Runge, and P.W. Sherman. 2002. Ecological and evolutionary traps. *Trends Ecol Evol* 17:474–480.
- Schlesinger M.D., P.N. Manley, and M. Holyoak. 2008. Distinguishing stressors acting on land bird communities in an urbanizing environment. *Ecology* 89:2302–2314.

- Schoech S.J. and R. Bowman. 2003. Does differential access to protein influence differences in timing of breeding of Florida scrub-jays (*Aphelocoma coerulescens*) in suburban and wildland habitats? *Auk* 120:1114–1127.
- Seewagen C.L., C.D. Sheppard, E.J. Slayton, and C.G. Guglielmo. 2011. Plasma metabolites and mass changes of migratory landbirds indicate adequate stopover refueling in a heavily urbanized landscape. *Condor* 113:284–297.
- Smith S.B. and S. R. McWilliams. 2010. Patterns of fuel use and storage in migrating passerines in relation to fruit resources at autumn stopover sites. *Auk* 127:108–118.
- Smith S.B., S.R. McWilliams, and C.G. Guglielmo. 2007. Effect of diet composition on plasma metabolite profiles in a migratory songbird. *Condor* 109:48–58.
- Suarez-Rubio M., P. Leimgruber, and S. C. Renner. 2011. Influence of exurban development on bird species richness and diversity. *J Ornithol* 152:461–471.
- Suarez-Rubio M., S. Wilson, P. Leimgruber, and T. Lookingbill. 2013. Threshold responses of forest birds to landscape changes around exurban development. *PLoS ONE* 8:e67593.
- Suorsa P., H. Helle, V. Koivunen, E. Huhta, A. Nikula, and H. Hallarainen. 2004. Effects of forest patch size on physiological stress and immunocompetence in an area sensitive passerine, the Eurasian treecreeper: an experiment. *Proc R Soc B* 271:435–440.
- Suorsa P., E. Huhta, A. Nikula, M. Nikinmaa, A. Jantti, H. Helle, and H. Hakkarainen. 2003. Forest management is associated with physiological stress in an old growth forest passerine. *Proc R Soc B* 270:963–969.
- Theobald D.M. 2001. Land use dynamics beyond the American urban fringe. *Geogr Rev* 91:544–64.
- . 2005. Landscape patterns of exurban growth in the USA from 1980 to 2020. *Ecol Soc* 10:32.
- Van Horn B. 1983. Density as a misleading indicator of habitat quality. *J Wildl Manage* 47:893–901.
- Wade A.A. and D.M. Theobald. 2009. Residential development encroachment on US protected areas. *Conserv Biol* 24:151–161.
- Wikelski M. and S. J. Cooke. 2006. Conservation physiology. *Trends Ecol Evol* 21:38–46.
- Wood E.M., A.M. Pidgeon, V.C. Radeloff, D.P. Helmers, P.D. Culbert, N.S. Keuler, and C.H. Flather. 2014. Housing development erodes avian community structure in U.S. protected areas. *Ecol Appl* 24:1445–1462.
- Zanette L.Y., P. Doyle, and S.M. Trémont. 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* 81:1654–1666.
- Zanette L.Y., A.F. White, M.C. Allen, and M. Clinchy. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. *Science* 334:1398–1401.