

Site Fidelity and Lifetime Territorial Consistency of Ovenbirds (*Seiurus aurocapilla*) in a Contiguous Forest

Author(s) :Michael J. Bernard, Laurie J. Goodrich, Walter M. Tzilkowski, and Margaret C. Brittingham

Source: The Auk, 128(4):633-642. 2011.

Published By: The American Ornithologists' Union

URL: <http://www.bioone.org/doi/full/10.1525/auk.2011.10206>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.



SITE FIDELITY AND LIFETIME TERRITORIAL CONSISTENCY OF OVENBIRDS (*SEIURUS AUROCAPILLA*) IN A CONTIGUOUS FOREST

MICHAEL J. BERNARD,^{1,3} LAURIE J. GOODRICH,² WALTER M. TZILKOWSKI,¹
AND MARGARET C. BRITTINGHAM¹

¹School of Forest Resources, Penn State University, 433 Forest Resources Building, University Park, Pennsylvania 16802, USA; and

²Hawk Mountain Sanctuary Association, Acopian Center for Conservation Learning, 410 Summer Valley Road, Orwigsburg, Pennsylvania 17961, USA

ABSTRACT.—We investigated territory-level habitat use patterns of 132 color-banded male Ovenbirds (*Seiurus aurocapilla*) over a 12-year period at Hawk Mountain Sanctuary in eastern Pennsylvania. Our primary goals were to test hypotheses concerning selection behavior as well as to describe territory fidelity of an area-sensitive Neotropical migrant by quantifying year-to-year movements of individuals over a period equivalent to several generations. Furthermore, we tested whether returns and territory shifts were associated with prior reproductive success and bird age. We measured occupancy as the number of birds that occupied 60-m grid cells that covered two 18-ha study sites over the 12-year period and similarly calculated rates of reproductive success within each grid cell. Rates of reproductive success were generally high (>60%) and were not correlated with occupancy rates. Return rates also were high, and birds rarely moved far from their first territory (mean = 68 m) during their lifetimes. There was no relationship between site fidelity and past reproductive success, but shift distances decreased with age. Our results differed from past studies that found a relationship between breeding dispersal and past reproductive success for species in a number of habitats. High territory fidelity regardless of past reproductive performance may represent a general case for songbirds breeding in homogeneous, high-quality habitats in which sources of failure are infrequent and unpredictable. In such cases, the potential benefit of moving may not outweigh the costs, and being able to obtain and maintain a territory may be of prime importance. Received 28 August 2010, accepted 18 July 2011.

Key words: decision rules, occupancy, Ovenbird, *Seiurus aurocapilla*, site fidelity, territory fidelity, territory shift.

Fidelidad al Sitio y Consistencia Territorial durante la Vida en *Seiurus aurocapilla* en un Bosque Continuo

RESUMEN.—Investigamos los patrones de uso de hábitat en el nivel de territorio de 132 individuos machos de *Seiurus aurocapilla* marcados con anillas coloridas durante 12 años en el santuario Hawk Mountain en el este de Pennsylvania. Nuestros principales objetivos fueron poner a prueba hipótesis sobre el comportamiento de selección, así como describir la fidelidad a los territorios de un ave migratoria neotropical sensible a la reducción de tamaño del hábitat, mediante la cuantificación de los movimientos año a año de los individuos durante un período equivalente a varias generaciones. Además, probamos si los retornos y los cambios de territorio, se asociaron con el éxito antes de la reproducción y con la edad de las aves. Medimos la ocupación como el número de aves que ocupan una celda de una cuadrícula de 60-m que cubre dos sitios de estudio de 18 ha durante un período de 12 años y también calculamos las tasas de éxito reproductivo dentro de cada celda de la cuadrícula. Las tasas de éxito reproductivo fueron generalmente elevadas (> 60%) y no se correlacionaron con las tasas de ocupación. Las tasas de retorno también fueron altas, y las aves se movieron rara vez lejos de su primer territorio (media = 68 m) durante su vida. No hubo relación entre la fidelidad al sitio y el éxito reproductivo pasado, pero las distancias de desplazamiento disminuyeron con la edad. Nuestros resultados difirieron de estudios anteriores que encontraron una relación entre la dispersión reproductiva y el éxito reproductivo pasado para diferentes especies en una serie de hábitats. Una alta fidelidad al territorio, independientemente del desempeño reproductivo en el pasado puede representar un caso general para las aves canoras que se reproducen en hábitats homogéneos y de alta calidad en los que las posibilidades de fracaso son escasas e impredecibles. En tales casos, el beneficio potencial de moverse no compensa el costo, y ser capaz de obtener y mantener un territorio puede ser de gran importancia.

RESOURCE VARIATION AMONG and within habitats can influence the reproductive performance of individuals and populations, resulting in trends whereby habitats with a favorable combination of resources are consistently more productive over time. Thus, there

is considerable selective pressure on highly mobile organisms for the ability to assess conditions and make habitat choices that maximize fitness (Fretwell and Lucas 1970). Additionally, individuals that survive multiple years may make adjustments between

³E-mail: mbernar7@jhu.edu

seasons as they decide whether to reuse sites and specific territories that they occupied previously or disperse in search of a better locale (Hoover 2003, Howlett and Stutchbury 2003, Morton 2005).

Cases in which migratory birds returned to previous territories after drastic habitat alterations (Hildén 1965, Wiens et al. 1986) have led some researchers to consider site fidelity a rigid behavior that counteracts “ideal” habitat selection in older individuals (Johnson 2007). However, there is strong evidence that the decision to return or move away (disperse) from a former site is the result of adaptive responses to habitat conditions. Reusing a former territory reduces search costs (Stamps et al. 2005), such as a higher risk of mortality during the search period or reduction in available time that could have been allocated to breeding activities. In addition, familiarity may enable individuals to use resources more efficiently and provide other advantages, assuming that habitat conditions are relatively stable over time (Greenwood and Harvey 1982). However, for individuals that occupy low-quality sites, it may be beneficial to endure search costs to find a better location. In any case, the probability of dispersing to a new territory or returning to the territory used previously should be related to the cost of movement in relation to the benefits gained (Switzer 1993).

The “decision rules” hypothesis states that birds use past experience to decide which strategy to employ, thus explaining observations that birds that fail to produce young during one year return to the same breeding site the next year at lower rates or disperse farther than birds that bred successfully (Harvey et al. 1979, Weatherhead and Boak 1986, Gavin and Bollinger 1988, Payne and Payne 1993, Catlin et al. 2005). Experiments that manipulated breeding success provide strong support for a causal link between failure and dispersal (Bollinger and Gavin 1989, Haas 1998, Hoover 2003). However, other observational studies have failed to show this relationship (e.g., Krebs 1971, Bédard and LaPointe 1984). Switzer (1993) suggested that whether an individual should move to a new territory following reproductive failure or return to a territory used previously should depend on both the predictability of the reproductive outcome (e.g., poor territories were consistently worse than good territories), the variability among available territories, and the benefits of moving in relation to costs.

There is great interest in understanding habitat use and selection at both a theoretical level and for applied aspects of conservation and management (Pulliam and Danielson 1991, Jones 2001, Ahlering and Faaborg 2006, Hallworth et al. 2008, Cornell and Donovan 2010). Habitat use patterns are the end result of the habitat selection process (Jones 2001) and consequently provide insights into habitat selection behavior. We investigated territory-level habitat use patterns of the Ovenbird (*Seiurus aurocapilla*) using measures of occupancy (Sergio and Newton 2003), reproductive success, and between-year territory movements of individuals collected over a 12-year period from a population of uniquely color-banded males at Hawk Mountain Sanctuary in eastern Pennsylvania. Our data set allowed us to examine long-term habitat use patterns in individuals of known age and with known histories of reproductive performance. Our primary goals were to use this long-term data set to test hypotheses concerning selection behavior as well as to describe territory fidelity behavior of a forest-dependent Neotropical migrant breeding within

contiguous forest habitat. We did this by quantifying year-to-year movements of individuals over the course of their lifetimes, and tested whether returns and territory shifts were associated with prior reproductive success and bird age.

METHODS

Study sites.—Our study was conducted at two forested sites, Owl’s Head (OH) and River of Rocks (RR), at Hawk Mountain Sanctuary (40°38’N and 75°59’W) in eastern Pennsylvania (Fig. 1). Hawk Mountain Sanctuary is part of a 10,000-ha tract of second-growth mixed deciduous forest that comprises public and private lands. Hawk Mountain Sanctuary researchers established the study sites as Breeding Bird Census (BBC) plots in 1982 to monitor bird diversity (Goodrich et al. 1998). The sites are 1.5 km apart and each contains grid points (238 and 210 at Owl’s Head and River of Rocks, respectively) marked at 30.5-m intervals (Fig. 1). The distance between grid points was established to facilitate spot-mapping of birds. Owl’s Head (490 × 400 m, 19.4 ha) sits at an elevation of 440 m on the southwest-facing mountainside. River of Rocks (430 × 400 m, 16.9 ha) sits on the east-facing side of the ridge and varies in elevation from 275 to 335 m (Goodrich et al. 1998).

There are considerable structural differences between sites. Owl’s Head has a more gradual slope, lower canopy height, higher shrub density, and more small trees occupying space in the understory than River of Rocks, which has lower vegetative groundcover and higher rock cover. Dominant overstory species at both sites include Chestnut Oak (*Quercus prinus*), Red Oak (*Q. rubra*), Red Maple (*Acer rubrum*), Scarlet Oak (*Q. coccinea*), Sweet Birch (*Betula lenta*), and White Oak (*Q. alba*). Pitch Pine (*Pinus rigida*), Eastern White Pine (*P. strobus*), and Eastern Hemlock (*Tsuga canadensis*) occur in low densities. The shrub layer is composed of Black Huckleberry (*Gaylussacia baccata*), blueberry (*Vaccinium* spp.), Sheep Laurel (*Kalmia angustifolia*), Mountain Laurel (*K. latifolia*), and Wintergreen (*Gaultheria procumbens*). Canopy trees at both sites range in age from 120 to 200 years. Excluding a 0.8-ha section of OH that was cut in the mid-1970s, the sites have remained relatively undisturbed over the past century (Goodrich et al. 1998). Bernard (2010) provides a more detailed summary of the habitat features of the study sites.

Bird surveys.—Hawk Mountain Sanctuary researchers began color-banding male Ovenbirds in 1988 using OH and RR as control sites for a large-scale study investigating population dynamics in a fragmented landscape (Porneluzi et al. 1993, L. J. Goodrich et al. unpubl. data). Researchers stopped banding at all sites in 1996 after completion of the forest fragmentation study. Banding resumed at OH and RR in 1998 and data collection continued through 2009. We chose to use the final 12 years for our study period because the consistency in data collection allowed for comparisons among years, and we avoided complications from the pause in banding during the 1996 and 1997 seasons. During the 12-year study period, there were 132 banded (76 OH, 56 RR) male birds with territories on the study sites. In addition, there were 47 unbanded male-years (30 OH, 17 RR). The actual number of unbanded males on our sites may have been less than 47 if unbanded birds returned multiple years. All but 20 males were banded as second-year (SY) birds, so the true number of unbanded males ranged from 27 to 47.

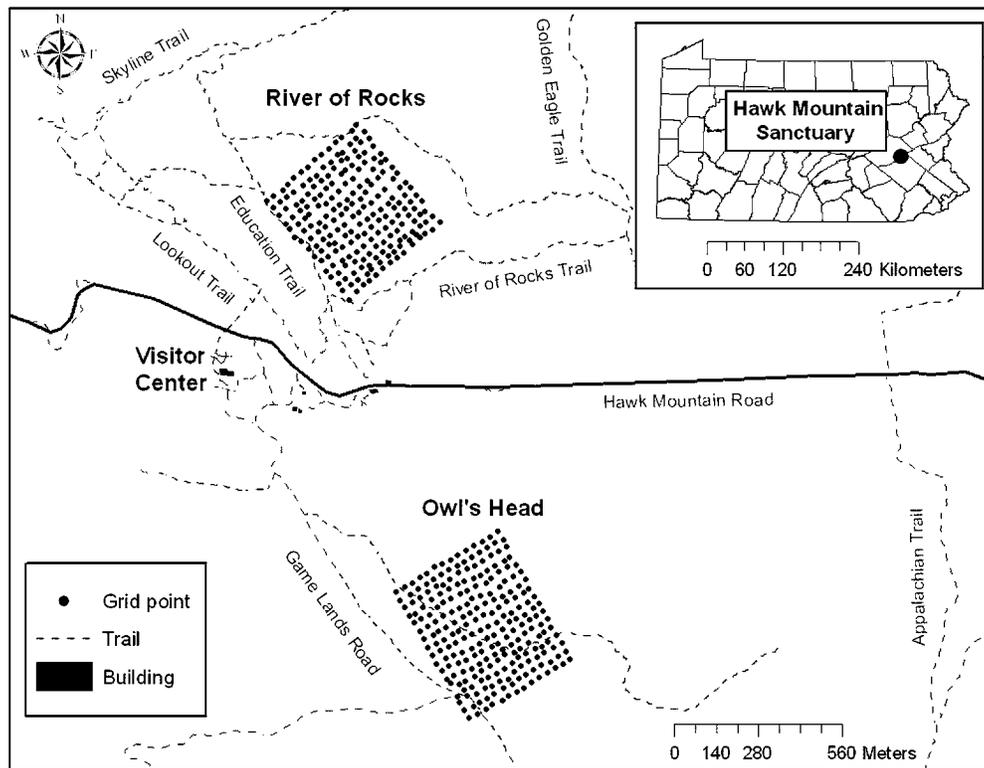


FIG. 1. Location of Hawk Mountain Sanctuary in eastern Pennsylvania (inset) and Owl's Head (OH) and River of Rocks (RR) study sites at Hawk Mountain Sanctuary. Grid points used for spot-mapping censuses are marked in the field by flagging tape and labeled alphanumerically.

In Pennsylvania, male Ovenbirds arrive in late April and establish territories before females arrive ~1 week later (Porneluzi et al. 1993, Goodrich et al. 1998). Researchers captured males early in the breeding season using mist nets and song playback accompanied by a wooden decoy. Birds were aged as either SY or after-second-year (ASY) birds according to plumage coloration and rectrice shape (Donovan and Stanley 1995, Pyle 1997). Each bird received a federal band with three color bands in a unique combination.

Throughout the breeding season, from May through mid-July, researchers conducted bird surveys during approximately 0530–1000 hours EST several mornings per week by spot-mapping the locations of singing males and observing their behavior, including singing behavior and border disputes (Bibby et al. 1992). Males display territorial behavior throughout the period of morning song and give chase to intruding males (Hann 1937, Van Horn and Donovan 1994). Territories remain fixed throughout the breeding season, but territorial defense is less rigorous late in the season when fledglings leave the nest (Hann 1937, Stenger and Falls 1959). Each bird survey covered an entire study site, and observers used grid markings in the field (flagging tape on trees) to plot locations of birds identified by band combination on a map of the study site (Howlett and Stutchbury 1997, Morton 2005). Researchers visited territories at different times of the morning in case the activity of individuals varied temporally.

Females lay eggs in May, which hatch from late May through June. Ovenbirds are single-brooded, but they may renest after failure (Van Horn and Donovan 1994). Fledglings leave the nest

~8 days after hatching and are semidependent for 30 days (Hann 1937). During this fledgling period, which spans from mid-June through mid-July, fledglings can be observed in close association with parents (Porneluzi et al. 1993). Researchers visited each territory approximately every 4 days during the fledgling period and classified birds as “successful” if banded adults were observed feeding, defending, or interacting closely with at least one fledgling (Howlett and Stutchbury 2003, Hallworth et al. 2008). Thus, “reproductive success” here refers to the success of the territorial male over the entire breeding season and is not directly comparable to true nest success, which is based on each nesting attempt (Mayfield 1961, Dinsmore et al. 2002). Nevertheless, our measure of success was comparable to other studies that categorized individuals as successful if any of their nest attempts produced one fledgling (Bollinger and Gavin 1989, Haas 1998, Howlett and Stutchbury 2003, Bakermans and Rodewald 2006, Hallworth et al. 2008).

Parasitism by Brown-headed Cowbirds (*Molothus ater*; hereafter “cowbirds”) was not a large threat on the two study sites because cowbirds occurred infrequently. Both sites were surveyed annually since 1982 using standard Breeding Bird Census spot-mapping techniques as part of a long-term monitoring program (Goodrich et al. 1998). Cowbirds were absent from OH and found in very low densities at RR (0.65 ± 0.51 males 10 ha^{-1}) (D. R. Barber and L. J. Goodrich unpubl.data). Because cowbirds are significantly larger than Ovenbird young, they were easy to detect during fledgling observations and were noted when they were observed.

Porneluzi et al. (1993) noted that an estimate of success based on observations of males during territory visits likely represents a minimum success rate, given that some individuals with fledglings may move off study sites and escape detection. To reduce this bias, we classified birds as “unsuccessful” only if they were observed a minimum of three times during the fledgling period (1 June–15 July) and were never observed with fledglings and showed no other behavioral cues indicating the presence or absence of young. Food-carrying provided insight into breeding status because males without nestlings or fledglings rarely carry food (Hann 1937, Van Horn and Donovan 1994). Males without young were less secretive and less defensive toward humans, and they often spent more time singing to advertise their territories. Successful birds often used defensive chipping to warn young of intruders, and fledglings often chipped in response to their parents during the first 2 weeks after leaving the nest (L. J. Goodrich pers. obs.). These behaviors allowed observers to identify territories on the study sites to target during later surveys until fledglings were observed in association with a parent.

We selected the cut-off of three independent observations because experience indicated that more observations were rarely needed to spot birds with fledglings. We visited each site multiple times per week during the entire breeding season, so we were very familiar with the location and behavior of individual males. During the fledgling period, we targeted males that had not been observed with fledglings and followed them for an extended period of time (often >1 h) to ensure that they were without fledglings. In addition, we had no males that were observed on ≥ 3 separate days during the fledgling period without young and then were later reported with young. We considered birds that we did not relocate on at least three different dates during the fledgling period to have “unknown” reproductive status and excluded them from analyses based on reproductive success.

Occupancy and success measures.—To measure habitat use and patterns of reproductive success at different locations on each site, we used a TDC1 Data Collector (Trimble, Sunnyvale, California) global positioning system (GPS) device to collect GPS coordinates of the grid points used for spot-mapping and plotted bird locations from every season onto maps of the study sites using the editor toolbar in ARCMAP (ARCGIS, version 9.2; ESRI, Redlands, California). We plotted locations of only those birds observed on at least three separate occasions and located within site boundaries at least once. We used Hawth's Tools (Beyer 2004) to construct a grid over both study sites using cell widths of 60 m so that grid cells were similar in size to Ovenbird territories. We calculated a within-season measure of use based on the number of different birds whose territories were located within a grid cell during a season.

Occupancy was calculated by summing the within-season measures over the 12-year study period (units = total bird-years). We calculated rates of reproductive success (success rates) at each grid cell by finding the mean success rate of all birds with known reproductive status that occupied a particular cell over the study period. We calculated Pearson's product-moment correlation coefficient between occupancy and success rates and tested for a correlation using the null hypothesis that the variables were uncorrelated (Sokal and Rohlf 1995).

Because we resampled birds that returned to the same cell in multiple years, our occupancy measure had the potential to be

greatly influenced by a small number of the longest-lived birds. To reduce concerns of temporal dependence, we also investigated patterns of habitat use by measuring how frequently a cell was occupied by a new bird after the permanent disappearance of the previous resident. For each year, grid cells of a nonreturning bird were treated as trials that resulted in either successes (use by another bird) or failures (no use) in the following year. A rate, termed the “new resident rate,” was calculated for each grid cell by dividing the number of successes by the total number of trials over the study period. We tested for a correlation between the new resident rate and success rates.

Fidelity measures.—Researchers believe that a proportion of birds that fail to return between breeding seasons are alive but have dispersed away from study areas (Greenwood 1980, Greenwood and Harvey 1982, Marshall et al. 2000). We assessed site fidelity by calculating apparent return rates of banded birds following their first year on each site. We considered a bird to have returned if researchers resighted it in the year after banding, regardless of whether its new territory was located within site boundaries. This measure is termed an “apparent return rate” (Marshall et al. 2000) because we did not adjust it on the basis of resighting probability using an extension of the Cormack-Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) approach. We considered that modeling detection probability was unnecessary, given our data, for several reasons. Birds that were alive and returned to the study area were unlikely to escape detection because researchers surveyed three territory widths (150–200 m) outside of the study sites several times during each season. In addition, no banded Ovenbird reported missing in one year was ever reobserved in a subsequent year, which resulted in a detection probability of 1. Over the 21-year banding period, no banded Ovenbirds moved between the study sites (~1.5 km; L. J. Goodrich unpubl. data) and few were banded as ASY birds, which suggests that long-distance dispersal by older birds was rare and that failures to return most likely resulted from death. If permanent emigration did occur on our sites, it was indistinguishable from death, using either apparent return rates or rates adjusted by the Cormack-Jolly-Seber approach. In a similar study, Murphy (1996) reported no differences between apparent return rates and return rates adjusted for detection probability of the Eastern Kingbird (*Tyrannus tyrannus*), a species that had high site fidelity and was easily located.

We tested for a relationship between first-year reproductive success and return rates using chi-square tests of independence (Sokal and Rohlf 1995). We excluded birds from analysis if they were banded before 1998 (5 OH, 0 RR) or during the last year of the study (1 OH, 2 RR). We assessed territory fidelity by estimating shift distance between territories (i.e., distance from territory in year t to year $t + 1$). We calculated a territory center for each territory by averaging the coordinates of each location. We measured shift distance as the distance (m) between territory centers. Seven birds with initial territories located at the boundary of the study sites were excluded from the analysis because their later territories fell outside of the study sites and could not be mapped with the same precision as territories within site boundaries.

We tested for differences in shift distance based on reproductive success and age using separate two-way mixed-model analyses of variance (ANOVA). To avoid resampling individuals, we used only first-year shifts (year 1 to year 2) to test the hypothesis

that successful birds would have higher rates of territory fidelity than unsuccessful birds. However, resampling birds was unavoidable when testing whether older birds were more faithful to previous territories than younger birds; therefore, we used a repeated-measures approach that treated birds as subjects. In both models, we included a random site factor to account for possible violations of the assumption of independence raised by correlation of variances among observations within each site. We assessed the significance of the fixed effect of interest (reproductive success or age) using a likelihood ratio test (LRT) comparing a full model that included the fixed effect of interest in addition to a fixed intercept and random site effect to a nested reduced model that excluded the fixed effect of interest (Bolker et al. 2008). We used maximum likelihood (ML) estimation for both models. Diagnostic plots and Levene's tests for homogeneity indicated that the residuals met the assumptions of normality and homoscedasticity.

Bird age, which was determined initially during banding, was compared among five age classes. The SY birds returning for their first breeding season were considered to be 1-year-olds and placed in the first age class. Birds banded as ASY were considered to be 2-year-olds. Birds advanced to a new age class every year; however, we grouped all birds that lived 5 years or more into the fifth age class. We used the Tukey-Kramer multiple-comparisons procedure (Sokal and Rohlf 1995) to test for differences in shift distance among age classes.

We quantified the degree of lifetime territorial consistency using a similar measure of shift distance. However, instead of relating each movement to a bird's previous-year territory, we related all shifts to the first-year territory. Thus, we calculated the distance between the first-year territory center and the center of every later territory during the period a bird returned (year 1 to year $t = 2, 3, \dots, n$, where $n =$ number of years a bird returned). Because few birds ($n = 9$) lived beyond 3 years at RR, we combined data from both sites. In order to better understand what shift distance would look like if birds moved randomly, we performed a simulation using 1,000 birds shifting in random directions (0–359 degrees) each year over 6 years (5 shifts). We randomly assigned shift distances from one year to the next using a bootstrapping approach (Efron and Tibshirani 1993) to resample between-year shift distances observed on the study sites. All shift distances within the observed range were included in the bootstrapping procedure. For each year, we found the distance to the first-year territory using trigonometric functions.

To test whether the observed and simulated patterns of territorial consistency were similar, we performed separate linear model regressions using the distance from the first-year territory center as the dependent variable and shift occasion as the independent variable. Because shift distances were likely to vary among birds, we used a mixed linear model for the observed data by adding a random bird effect. Significance of the estimated slope for the observed data was determined using an LRT that compared the full model to a reduced model containing only the random bird effect. A t -test (Sokal and Rohlf 1995) was used to test the significance of the slope parameter estimate from the simulated data. Distance to the first-year territory center was transformed using the square-root transformation for both models. We used a Student's t -test (Sokal and Rohlf 1995) to compare the estimated slope coefficients from each model to test whether the observed and simulated patterns were

similar. We analyzed all fidelity data using program R (R Foundation for Statistical Computing, Vienna) and present all error estimates as standard errors (SE).

RESULTS

At the site level over the 12 years, mean density of Ovenbirds was 1.1 ± 0.1 males ha^{-1} at OH and 0.7 ± 0.1 males ha^{-1} at RR. Mean reproductive success was 0.74 ± 0.03 at OH and 0.75 ± 0.03 at RR. When birds whose reproductive outcome was classified as unknown (33 OH, 24 RR; see above) were classified as unsuccessful, reproductive success rates were 0.65 ± 0.05 and 0.61 ± 0.05 at each respective site.

Occupancy values of grid cells ranged from 4 to 20, with a mean of 14.0 ± 0.5 bird-years, at OH; and from 2 to 19, with a mean of 10.0 ± 0.6 bird-years, at RR. Success rates were not correlated with occupancy at either site (OH: $r = 0.21$, $df = 46$, $P = 0.15$; RR: $r = 0.13$, $df = 46$, $P = 0.39$) and were generally high at all levels of occupancy (Fig. 2A), with overall means of 0.74 ± 0.02 at both sites. There was a weak trend for reduced success rates at RR for cells with occupancy values below 8 bird-years, but only 6% of cells (3 of 48) at RR and 0% of cells at OH had success rates < 0.50 . Variation in individual survival influenced occupancy values as the residency period of the longest-lived bird within a cell tended to be much higher in cells with greater occupancy values (Fig. 2B). Thus, a particular cell had a higher occupancy value because it was associated with a bird that returned over multiple years and continued to use that territory. Mean new-resident rates were $87.4 \pm 4.1\%$ and $68.2 \pm 4.5\%$ at OH and RR, respectively, and there was no evidence for a correlation between success rates and new-resident rates (OH: $r = 0.18$, $df = 43$, $P = 0.25$; RR: $r = 0.16$, $df = 47$, $P = 0.26$).

Fidelity measures.—The majority of birds banded at OH (61 of 71) and RR (36 of 46) during the study period were SY birds returning for their first season of breeding. Return rates following the first year were high (Table 1) and independent of past

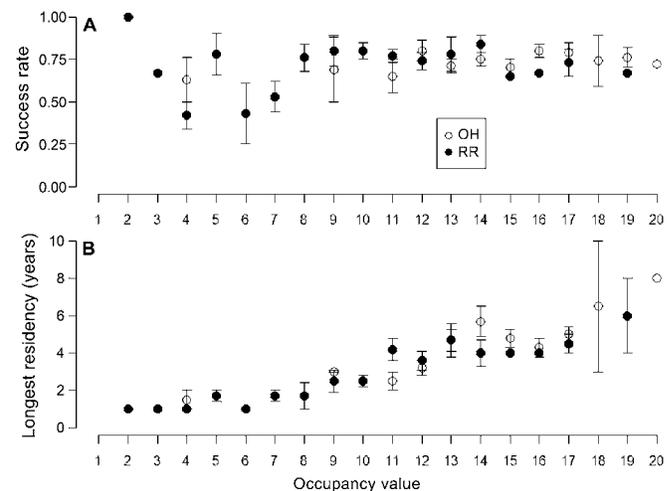


FIG. 2. (A) Mean (\pm SE) success rates (proportion successful) of Ovenbirds in cells at each occupancy level (total bird-years) at Owl's Head (OH) and River of Rocks (RR) study sites at Hawk Mountain Sanctuary, Pennsylvania, during the 12-year study period, 1998–2009. (B) Mean (\pm SE) longest residency period (years an individual used the same cell) at each occupancy level.

TABLE 1. Return rates of Ovenbirds banded between 1998 and 2008 at Owl's Head (OH) and River of Rocks (RR) study sites at Hawk Mountain Sanctuary, Pennsylvania, following their first year. Birds were grouped on the basis of reproductive performance during the first year.

Bird status	OH		RR	
	<i>n</i>	Proportion returned	<i>n</i>	Proportion returned
Successful	45	0.667	33	0.606
Unsuccessful	12	0.833	9	0.556
Unknown	13	0.846	12	0.500
Combined	70	0.729	54	0.574

TABLE 2. Distribution of the number of years banded Ovenbirds returned to Owl's Head (OH) and River of Rocks (RR) study sites at Hawk Mountain Sanctuary, Pennsylvania, during the 12-year study period, 1998–2009. Birds banded prior to 1998 (5 OH, 0 RR) or during the last year (1 OH, 2 RR) were not counted. Sixteen birds (14 OH, 2 RR) included were alive at the end of the 2009 season.

Years on site	Number of birds	
	OH	RR
1	19	23
2	12	12
3	14	10
4	7	3
5	8	3
6	3	1
7	2	2
8	2	0
9	2	0
10	0	0
11	1	0
Total	70	54

reproductive success (OH: $\chi^2 = 1.26$, $df = 1$, $P = 0.26$; RR: $\chi^2 = 0.07$, $df = 1$, $P = 0.78$). Similar results were observed when all birds with unknown reproductive status were treated as unsuccessful (OH: $\chi^2 = 2.44$, $df = 1$, $P = 0.12$; RR: $\chi^2 = 0.36$, $df = 1$, $P = 0.55$). Birds frequently returned to the study sites for >1 year (Table 2); mean number of years returned was 3.3 years at OH and 2.3 years at RR.

We used 44 OH and 24 RR birds to analyze shift distances between territories. Averaging within each site, mean first-year shift distance (year 1 to year 2) was 41.6 ± 5.4 m at OH and 76.5 ± 11.3 m at RR. Successful birds (OH: 39.4 ± 6.7 m, RR: 71.6 ± 13.5 m) did not move shorter distances than unsuccessful birds (OH: 30.9 ± 3.7 m, RR: 78.3 ± 18.7 m; LRT: $\chi^2 = 0.07$, $df = 1$, $P = 0.79$). Similar results were observed when we treated all birds with unknown reproductive status as unsuccessful (LRT: $\chi^2 = 0.06$, $df = 1$, $P = 0.81$). Shift distance (year t to year $t + 1$) differed among age classes (LRT: $\chi^2 = 14.9$, $df = 4$, $P < 0.01$); however, Tukey-Kramer comparisons indicated that first-year shifts were farther than shifts in all subsequent years ($P < 0.05$; Fig. 3). Shifts from age class 2 and later did not differ significantly ($P > 0.05$).

Using all SY and later territories ($n = 203$), birds moved a mean distance of 65.5 ± 3.6 m from their first-year territory (year 1 to year $t = 2, 3, \dots, n$, where $n =$ number of years a bird returned) during their lifetime on each site. Thirty-seven lifetime shifts were beyond 100 m,

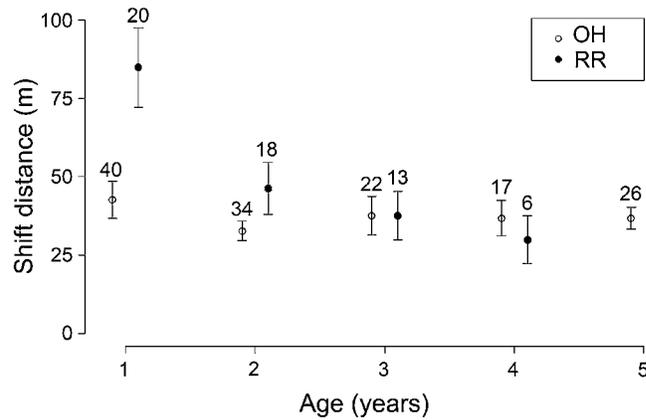


FIG. 3. Mean (\pm SE) shift distances (m) of Ovenbirds in different age classes at Owl's Head (OH) and River of Rocks (RR) sites at Hawk Mountain Sanctuary, Pennsylvania, during the 12-year study period, 1998–2009. Shifts by birds older than 5 years were placed in the final age class. Sample sizes are indicated above error bars.

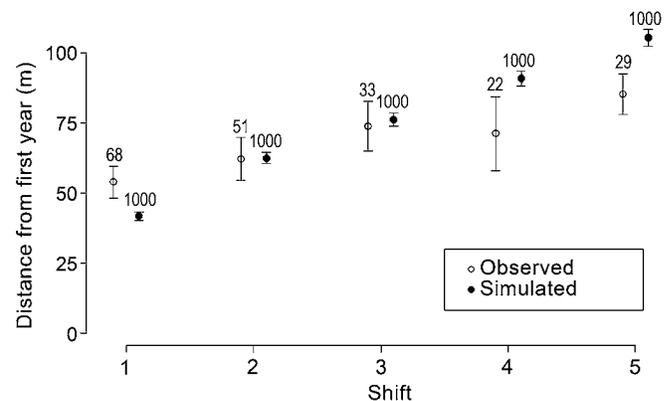


FIG. 4. Mean (\pm SE) distance (m) from first-year territory observed for each year Ovenbirds returned to study sites at Hawk Mountain Sanctuary, Pennsylvania, during the 12-year study period, 1998–2009, and for returns simulated by assigning random shift directions each year using 1,000 birds. All shifts beyond the fifth year were placed in the final grouping. Sample sizes are indicated above error bars.

the longest being 302.8 m. The regression model of the observed pattern of shifts indicated that the distance from the first-year territory increased each year birds returned to the sites (LRT: $\chi^2 = 12.6$, $df = 1$, $P < 0.01$). Thus, despite high rates of territory fidelity during consecutive years, territories tended to drift apart (Fig. 4). Territory maps did not indicate that birds moved away from their first-year territory in a constant direction, and a similar positive relationship (Fig. 4) was produced by the random shift simulation ($t = 79.6$, $df = 5,998$, $P < 0.01$), though the slope estimated from the simulation was steeper than that from the observed data ($t = 11.9$, $df = 6,199$, $P < 0.01$).

DISCUSSION

The high rates of reproductive success and returns observed in the present investigation were in accordance with past studies

conducted at OH and RR and other locations within contiguous forest habitat, which found Ovenbirds to occur and succeed at high rates in large tracts of mature deciduous forest (Porneluzi et al. 1993, Villard et al. 1993, Burke and Nol 1998, Porneluzi and Faaborg 1999, Bayne and Hobson 2001a). Rates of reproductive success within grid cells varied little ($CV < 3\%$) over both study sites, and the vast majority of cells ($>97\%$) had success rates >0.50 , indicating that reproductive success was high throughout the sites.

Occupancy varied considerably throughout both study sites, but it was not correlated with success rates as predicted. Instead, individual differences in life span strongly influenced occupancy scores as the grid cells with the highest scores often were part of the territories of the longest-lived birds on each site because birds moved little between years. These birds may have had traits that allowed them to survive longer than most of the population because success rates of grid cells that they occupied did not differ from other locations on the study sites occupied by shorter-lived birds. Differences in bird quality may explain differences in life span or even lifetime productivity, but long-lived birds did not occupy inherently better territories.

The lack of a correlation between occupancy and success rates differs from many other studies in which occupancy was a reliable measure of habitat quality primarily because birds tended to use between-year shifts to move to sites with higher long-term measures of productivity or reproductive success (Krebs 1971, Møller 1982, Beletsky and Orians 1987, Matthysen 1990, Forero et al. 1999, Sergio and Newton 2003, Espie et al. 2004). Our results may differ because the Ovenbirds we followed were in high-quality and fairly homogeneous habitats. By contrast, shifts to better territories generally are reported from heterogeneous habitats where there are pronounced differences in territory quality (Krebs 1971, Beletsky and Orians 1987). Our results suggest that occupancy may not be a reliable measure of habitat quality in relatively homogeneous habitats, and reaffirms Johnson's (2007) recommendation that researchers should use caution when using indices or surrogates to estimate habitat quality instead of measuring it directly using demographic measurements.

Declines in return rates of males and females following experimentally induced breeding failure provide compelling evidence that individuals of some species may consider prior breeding performance when deciding whether to return to a site (Bollinger and Gavin 1989, Haas 1998, Hoover 2003). However, there was no evidence of such a pattern among male Ovenbirds in the present investigation. Birds returned to the study sites at high rates regardless of reproductive success, and they rarely moved far from their first territory during their lifetime. These results are similar to those reported for Ovenbirds in Saskatchewan, where male return rates in continuous forest sites were 62%, and 88% of returning males were relocated <100 m from their capture location in the previous year (Bayne and Hobson 2002), and in New Brunswick, where 69.1% of males returned to forest sites, and only two of 130 returning males ever held a territory >100 m from a previous territory (Haché and Villard 2010). Male Hooded Warblers (*Wilsonia citrina*) nesting within high-quality habitat also showed high rates of site and territory fidelity, and neither were correlated with prior reproductive performance (Howlett and Stutchbury 2003).

The benefits of reusing previous breeding sites and territories may not be the same across habitats that differ in quality, disturbance

regime, and degree of structural complexity and variation. Our findings suggest that male Ovenbirds in high-quality contiguous forest have high site and territory fidelity. However, other studies have reported that male Ovenbirds disperse at higher rates in small forest fragments in which reproductive success was low than in larger forest fragments (Bayne and Hobson 2002, L. J. Goodrich unpubl. data), which suggests that Ovenbirds are capable of adjusting their dispersal decision depending on characteristics of the habitat. Research on Black-throated Blue Warblers (*Dendroica caerulescens*) also suggests that the cues that birds use and base territory-settlement decisions on may vary with habitat type (Betts et al. 2008, Cornell and Donovan 2010). The patterns observed in these examples lend support to Switzer's (1993) contention that birds may use different decision rules depending on their habitat, adopting a strategy of unconditionally maintaining residency on homogeneous high-quality habitats or basing dispersal decisions upon reproductive performance in low-quality or highly heterogeneous habitats.

Switzer (1993) modeled site fidelity and found that the "always stay" strategy performed better than the "win-stay: lose-switch" strategy for individuals occupying unpredictable habitats with little variation in quality among territories. Habitat quality, as evidenced by success rates and occupancy rates, was high throughout OH and RR, and reproductive failure did not seem to be spatially or temporally autocorrelated. The primary cause of nest failure was likely predation (Porneluzi et al. 1993, Hoover et al. 1995, L. J. Goodrich unpubl. data), and researchers occasionally found nests destroyed by predators (L. J. Goodrich pers. obs). There is a diverse predator community at OH and RR consisting of a variety of birds, snakes, and mammals (Hoover et al. 1995), and patterns of nest predation tend to be unpredictable in predator-rich systems such as this (Filliater et al. 1994, Wilson and Cooper 1998). By contrast, Prothonotary Warblers (*Protonotaria citrea*) nesting where territory quality was predictable and heterogeneous used the "win-stay: lose-switch" strategy and consequently had return rates and territory shifts that differed on the basis of past reproductive performance (Hoover 2003).

In addition to assessing the quality of their own territories, birds may make broad assessments of neighboring areas to determine which strategy is most appropriate. Interestingly, Bollinger and Gavin (1989) reported that return rates of Bobolinks (*Dolichonyx oryzivorus*) were more highly correlated with overall site productivity than any other reproductive measure, and Hoover (2003) noted a tendency for unsuccessful birds to reuse the same territory if their neighbors had bred successfully. Both authors proposed that birds may consider the performance of their neighbors in addition to personal experience when deciding whether to reuse a breeding site. This mechanism could explain patterns of site fidelity at OH and RR because birds were likely to have several successful neighbors. However, alternative hypotheses, such as population pressure (Weatherhead and Boak 1986), opportunities for extrapair fertilizations (Howlett and Stutchbury 2003), or monitoring of resources (Smith and Shugart 1987) cannot be eliminated on the basis of the results presented here.

Birds tended to shift greater distances between their first and second years than in later years (year t to year $t + 1$); however, nearly all between-year shifts were less than territory-widths (territory diameter = 106 m, 128 m, and 205 m) reported from studies of Ovenbirds in contiguous forests (Stenger 1958, Bayne and Hobson 2001b, Mazerolle and Hobson 2004). Other studies have found that site fidelity increased with age (Greenwood and

Harvey 1982, Harvey et al. 1984, Montalvo and Potti 1992, Payne and Payne 1993, Newton 2001). Presumably, familiarity with a site may promote increasing site fidelity by allowing more efficient use of resources and make territory defense easier. Furthermore, social dominance increases with age in some species (Smith et al. 1980, Rohwer et al. 1981, Sherry and Holmes 1989, Sergio et al. 2009), which also may aid in territory defense. Payne and Payne (1993) even suggested that familiarity with neighbors may encourage birds to reuse former territories because establishing relationships with a new set of neighbors may entail greater expenditure of time and energy. In addition, if there is any cost associated with dispersal, the relative benefit in relation to cost will decrease as a bird ages because of a decrease in potential number of reproductive events to compensate for costs (Switzer 1993).

Although birds moved little between years and placed their territories in similar locations, they tended to move farther away from their first breeding territory each year they returned (year 1 to year $t = 2, 3, \dots, n$, where $n =$ number of years a bird returned). We may have predicted shifts to follow a directional pattern if there was a clear quality gradient on the study sites (e.g., transition from forest edge to core), but success rates were generally high at all locations. Furthermore, territory maps suggested that shifts did not follow a consistent direction, and the simulation that shifted birds in random directions produced a similar “territory drift” pattern. Had we located nests and color-banded females, we might have been able to determine whether small territory shifts were associated with changes in nest placement, mate changes, or both. These findings may further support the notion that quality was relatively homogenous over the study sites because there were no penalties to reproductive performance if birds did not return to the exact location of their previous territories.

Although both study sites had high success rates and high return rates that were similar to those reported from other studies of Ovenbirds breeding in large, contiguous forests, there were observable differences in these measures between our two study sites, due in part to the habitat structure of each site and also to a year effect that existed only at RR during the last years of the study. Several regions of RR (~2.2 ha) are dominated by large boulders, and rocks cover about 10× more space at RR ($22.5 \pm 0.5\%$) than at OH ($2.1 \pm 0.5\%$; Bernard 2010). The rocky terrain at RR likely limits the area of the forest floor available for foraging by Ovenbirds, resulting in increased territory sizes (means: 1.0 ha versus 0.5 ha; M. J. Bernard et al. unpubl. data) and lower density in comparison to OH. Thus, the larger shift distances observed at RR can be attributed to the larger territory sizes at that site.

The factors contributing to the reduced return rates at the RR site are less clear. Increased adult mortality, increased emigration, or a combination of both could have caused returns to be lower at RR than at OH. We have no data that directly support either hypothesis, but we do have evidence that conditions at RR have changed in recent years. Although densities at RR have been consistently lower than at OH, they have declined rapidly from 0.9 males ha^{-1} in 2002 to a constant 0.6 males ha^{-1} over the period from 2007 to 2009. Over that same period, reproductive success rates fell to below 0.60, no first-year birds ($n = 4$) returned, and only 8 of 15 older birds returned. During the prior period (1998–2006), success rates had been higher at RR than at OH (OH: 0.73; RR: 0.79), and return rates were more comparable to OH (OH: 0.69; RR: 0.62) than they were over the entire study period.

There have been no drastic physical disturbances at RR in recent years. Therefore, it is unknown whether the trend at RR represents a short-term aberration or a recent degradation in habitat quality. If increased emigration rates are occurring as a result of a decline in habitat quality at RR, such a response suggests that Ovenbirds are able to adjust their dispersal strategy rapidly in response to habitat changes that are more subtle than forest fragmentation.

In summary, our long-term study of Ovenbirds has shown that within high-quality, contiguous forest habitat, individuals appear to use an “always stay” strategy where they remain on a territory throughout their lifetime with minor shifts between years resulting in territorial drift over the lifetime of the individual. These results differ from other studies that have found a relationship between breeding dispersal and past reproductive success. High territory fidelity regardless of past reproductive performance may represent a general case for songbirds breeding in homogeneous, high-quality habitats, where sources of failure are infrequent and unpredictable. In such cases, the potential benefit of moving may not outweigh the costs and being able to obtain and maintain a territory may be of prime importance.

ACKNOWLEDGMENTS

We thank K. Bildstein, D. Barber, and past and present researchers, staff, and volunteers at Hawk Mountain for providing resources and support during the study. We also thank Penn State faculty M. Marshall and T. Wagner, and graduate students B. Fost, S. Pabian, G. Stokke, and A. Wilson, for advice and input on research design and data analysis. We thank field assistants A. Carter, K. Dibble, K. Stefan, and L. Simpson. We thank D. Dearborn and two anonymous reviewers for their helpful comments. Funding was provided by Pennsylvania’s Wild Resource Conservation Program, the Pennsylvania Agricultural Experiment Station, and Hawk Mountain Sanctuary Association. This paper is Hawk Mountain Sanctuary Contribution no. 203.

LITERATURE CITED

- AHLERING, M. A., AND J. FAABORG. 2006. Avian habitat management meets conspecific attraction: If you build it, will they come? *Auk* 123:301–312.
- BAKERMANS, M. H., AND A. D. RODEWALD. 2006. Scale-dependent habitat use of Acadian Flycatcher (*Empidonax vireescens*) in central Ohio. *Auk* 123:368–382.
- BAYNE, E. M., AND K. A. HOBSON. 2001a. Effects of habitat fragmentation on pairing success of Ovenbirds: Importance of male age and floater behavior. *Auk* 118:380–388.
- BAYNE, E. M., AND K. A. HOBSON. 2001b. Movement patterns of adult male Ovenbirds during the post-fledgling period in fragmented and forested boreal landscapes. *Condor* 103:343–351.
- BAYNE, E. M., AND K. A. HOBSON. 2002. Apparent survival of male Ovenbirds in fragmented and forested boreal landscapes. *Ecology* 83:1307–1316.
- BÉDARD, J., AND G. LAPOINTE. 1984. Banding returns, arrival times, and site fidelity in the Savannah Sparrow. *Wilson Bulletin* 96:196–205.
- BELETSKY, L. D., AND G. H. ORIANS. 1987. Territoriality among male Red-winged Blackbirds. I. Site fidelity and movement patterns. *Behavioral Ecology and Sociobiology* 20:21–34.

- BERNARD, M. 2010. Habitat selection, site fidelity, and lifetime territorial consistency of Ovenbirds in a contiguous forest. M.S. thesis, Pennsylvania State University, State College, Pennsylvania.
- BETTS, M. G., A. S. HADLEY, N. RODENHOUSE, AND J. J. NOCERA. 2008. Social information trumps vegetation structure in breeding-site selection by a migrant songbird. *Proceedings of the Royal Society of London, Series B* 275:2257–2263.
- BEYER, H. L. 2004. Hawth's Analysis Tools for ArcGIS. [Online.] Available at www.spatial-ecology.com/htools.
- BIBBY, C. J., N. D. BURGESS, AND D. A. HILL. 1992. *Bird Census Techniques*. Academic Press, London.
- BOLKER, B. M., M. E. BROOKS, C. J. CLARK, S. W. GEANGE, J. R. POULSEN, M. H. H. STEVENS, AND J. S. S. WHITE. 2008. Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–134.
- BOLLINGER, E. K., AND T. A. GAVIN. 1989. The effects of site quality on breeding-site fidelity in Bobolinks. *Auk* 106:584–594.
- BURKE, D. M., AND E. NOL. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *Auk* 115:96–104.
- CATLIN, D. H., D. K. ROSENBERG, AND K. L. HALEY. 2005. The effects of nesting success and mate fidelity on breeding dispersal in Burrowing Owls. *Canadian Journal of Zoology* 83:1574–1580.
- CORMACK, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438.
- CORNELL, K. L., AND T. M. DONOVAN. 2010. Scale-dependent mechanisms of habitat selection for a migratory passerine: An experimental approach. *Auk* 127:899–908.
- DINSMORE, S. J., G. C. WHITE, AND F. L. KNOPF. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- DONOVAN, T. M., AND C. M. STANLEY. 1995. A new method for determining Ovenbird age on the basis of rectrix shape. *Journal of Field Ornithology* 66:247–252.
- EFRON, B., AND R. J. TIBSHIRANI. 1993. *An Introduction to the Bootstrap*. CRC Press, Boca Raton, Florida.
- ESPIE, R. H. M., P. C. JAMES, L. W. OLIPHANT, I. G. WARKENTIN, AND D. J. LIESKE. 2004. Influence of nest-site and individual quality on breeding performance in Merlins *Falco columbarius*. *Ibis* 146:623–631.
- FILLIATER, T. S., R. BREITWISCH, AND P. M. NEALEN. 1994. Predation on Northern Cardinal nests: Does choice of nest site matter? *Condor* 96:761–768.
- FORERO, M. G., J. A. DONÁZAR, J. BLAS, AND F. HIRALDO. 1999. Causes and consequences of territory change and breeding dispersal distance in the Black Kite. *Ecology* 80:1298–1310.
- FRETWELL, S. D., AND H. L. LUCAS, JR. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16–36.
- GAVIN, T. A., AND E. K. BOLLINGER. 1988. Reproductive correlates of breeding-site fidelity in Bobolinks (*Dolichonyx oryzivorus*). *Ecology* 69:96–103.
- GOODRICH, L. J., C. B. VIVERETTE, S. E. SENNER, AND K. L. BILDSTEIN. 1998. Long-term use of Breeding Bird Census plots to monitor populations of Neotropical migrants breeding in deciduous forests in eastern Pennsylvania, USA. Pages 149–164 in *Forest Biodiversity in North, Central, and South America and the Caribbean: Research and Monitoring* (F. Dallmeier and J. A. Comiskey, Eds.). Parthenon, New York.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- GREENWOOD, P. J., AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13:1–21.
- HAAS, C. A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: An experimental approach. *Auk* 115:929–936.
- HACHÉ, S., AND M. A. VILLARD. 2010. Age-specific response of a migratory bird to an experimental alteration of its habitat. *Journal of Animal Ecology* 79:897–905.
- HALLWORTH, M., A. UELAND, E. ANDERSON, J. D. LAMBERT, AND L. REITSMA. 2008. Habitat selection and site fidelity of Canada Warblers (*Wilsonia canadensis*) in central New Hampshire. *Auk* 125:880–888.
- HANN, H. W. 1937. Life history of the Ovenbird in southern Michigan. *Wilson Bulletin* 44:146–235.
- HARVEY, P. H., P. J. GREENWOOD, B. CAMPBELL, AND M. J. STENNING. 1984. Breeding dispersal of the Pied Flycatcher (*Ficedula hypoleuca*). *Journal of Animal Ecology* 53:727–736.
- HARVEY, P. H., P. J. GREENWOOD, AND C. M. PERRINS. 1979. Breeding area fidelity of the Great Tit (*Parus major*). *Journal of Animal Ecology* 48:305–313.
- HILDÉN, O. 1965. Habitat selection in birds. *Annales Zoologici Fennici* 2:53–75.
- HOOVER, J. P. 2003. Decision rules for site fidelity in a migratory bird, the Prothonotary Warbler. *Ecology* 84:416–430.
- HOOVER, J. P., M. C. BRITTINGHAM, AND L. J. GOODRICH. 1995. Effects of forest patch size on nesting success of Wood Thrushes. *Auk* 112:146–155.
- HOWLETT, J. S., AND B. J. M. STUTCHBURY. 1997. Within-season dispersal, nest-site modification, and predation in re-nesting Hooded Warblers. *Wilson Bulletin* 109:643–649.
- HOWLETT, J. S., AND B. J. M. STUTCHBURY. 2003. Determinants of between-season site, territory, and mate fidelity in Hooded Warblers (*Wilsonia citrina*). *Auk* 120:457–465.
- JOHNSON, M. D. 2007. Measuring habitat quality: A review. *Condor* 109:489–504.
- JOLLY, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration–stochastic model. *Biometrika* 52:225–247.
- JONES, J. 2001. Habitat selection studies in avian ecology: A critical review. *Auk* 118:557–562.
- KREBS, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. *Ecology* 52:3–22.
- MARSHALL, M. R., R. R. WILSON, AND R. J. COOPER. 2000. Estimating survival of Neotropical–Nearctic migratory birds: Are they dead or just dispersed? Pages 195–199 in *Strategies for Bird Conservation: The Partners in Flight Planning Process* (R. Bonney, D. N. Pashley, R. J. Cooper, and L. Niles, Eds.). U.S. Department of Agriculture, Forest Service General Technical Report RMRS-P-16.
- MATTHYSEN, E. 1990. Behavioral and ecological correlates of territory quality in the Eurasian Nuthatch (*Sitta europaea*). *Auk* 107:86–95.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255–261.
- MAZEROLLE, D. F., AND K. A. HOBSON. 2004. Territory size and overlap in male Ovenbirds: Contrasting a fragmented and

- contiguous boreal forest. *Canadian Journal of Zoology* 82:1774–1781.
- MØLLER, A. P. 1982. Characteristics of magpie *Pica pica* territories of varying duration. *Ornis Scandinavica* 13:94–100.
- MONTALVO, S., AND J. POTTI. 1992. Breeding dispersal in Spanish Pied Flycatchers *Ficedula hypoleuca*. *Ornis Scandinavica* 23:491–498.
- MORTON, E. S. 2005. Predation and variation in breeding habitat use in the Ovenbird, with special reference to breeding habitat selection in northwestern Pennsylvania. *Wilson Bulletin* 117:327–335.
- MURPHY, M. T. 1996. Survivorship, breeding dispersal and mate fidelity in Eastern Kingbirds. *Condor* 98:82–92.
- NEWTON, I. 2001. Causes and consequences of breeding dispersal in the Sparrowhawk *Accipiter nisus*. *Ardea* 89(special issue):143–154.
- PAYNE, R. B., AND L. L. PAYNE. 1993. Breeding dispersal in Indigo Buntings: Circumstances and consequences for breeding success and population structure. *Condor* 95:1–24.
- PORNELUZI, P., J. C. BEDNARZ, L. J. GOODRICH, N. ZAWADA, AND J. HOOVER. 1993. Reproductive performance of territorial Ovenbirds occupying forest fragments and a contiguous forest in Pennsylvania. *Conservation Biology* 7:618–622.
- PORNELUZI, P., AND J. FAABORG. 1999. Season-long fecundity, survival, and viability of Ovenbirds in fragmented and unfragmented landscapes. *Conservation Biology* 13:1151–1161.
- PULLIAM, H. R., AND B. J. DANIELSON. 1991. Sources, sinks, and habitat selection: A landscape perspective on population dynamics. *American Naturalist* 137:S50–S66.
- PYLE, P. 1997. *Identification Guide to North American Birds, Part 1: Columbidae to Ploceidae*. Slate Creek Press, Bolinas, California.
- ROHWER, S. A., P. W. EWALD, AND F. C. ROHWER. 1981. Variation in size, dominance and appearance within and between sex and age classes in Harris' Sparrows. *Journal of Field Ornithology* 52:291–303.
- SEBER, G. A. F. 1965. A note on the multiple-recapture census. *Biometrika* 52:249–259.
- SERGIO, F., J. BLAS, AND F. HIRALDO. 2009. Predictors of floater status in a long-lived bird: A cross-sectional and longitudinal test of hypotheses. *Journal of Animal Ecology* 78:109–118.
- SERGIO, F., AND I. NEWTON. 2003. Occupancy as a measure of territory quality. *Journal of Animal Ecology* 72:857–865.
- SHERRY, T. W., AND R. T. HOLMES. 1989. Age-specific social dominance affects habitat use by breeding American Redstarts (*Setophaga ruticilla*): A removal experiment. *Behavioral Ecology and Sociobiology* 25:327–333.
- SMITH, J. N. M., R. D. MONTGOMERIE, M. J. TAITT, AND Y. YOMTOV. 1980. A winter feeding experiment on an island Song Sparrow population. *Oecologia* 47:164–170.
- SMITH, T. M., AND H. H. SHUGART. 1987. Territory size variation in the Ovenbird: The role of habitat structure. *Ecology* 68:695–704.
- SOKAL, R. R., AND R. J. ROHLF. 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*, 3rd ed. W.H. Freeman, New York.
- STAMPS, J. A., V. V. KRISHNAN, AND M. L. REID. 2005. Search costs and habitat selection by dispersers. *Ecology* 86:510–518.
- STENGER, J. 1958. Food habits and available food of Ovenbirds in relation to territory size. *Auk* 75:335–346.
- STENGER, J., AND J. B. FALLS. 1959. The utilized territory of the Ovenbird. *Wilson Bulletin* 71:125–140.
- SWITZER, P. V. 1993. Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology* 7:533–555.
- VAN HORN, M. A., AND T. M. DONOVAN. 1994. Ovenbird (*Seiurus aurocapilla*). In *The Birds of North America*, no. 88 (A. Poole, Ed.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- VILLARD, M. A., P. R. MARTIN, AND C. G. DRUMMOND. 1993. Habitat fragmentation and pairing success in the Ovenbird (*Seiurus aurocapillus*). *Auk* 110:759–768.
- WEATHERHEAD, P. J., AND K. A. BOAK. 1986. Site infidelity in Song Sparrows. *Animal Behaviour* 34:1299–1310.
- WIENS, J. A., J. T. ROTENBERRY, AND B. VAN HORNE. 1986. A lesson in the limitations of field experiments: Shrubsteppe birds and habitat alteration. *Ecology* 67:365–376.
- WILSON, R. R., AND R. J. COOPER. 1998. Acadian Flycatcher nest placement: Does placement influence reproductive success? *Condor* 100:673–679.

Associate Editor: D. C. Dearborn