Population density affects foraging behavior of male Black-throated Blue Warblers during the breeding season

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ABSTRACT. Foraging behavior often reflects food availability, a resource that may increasingly limit breeding birds as intraspecific crowding increases. Measuring foraging behavior, therefore, provides a way to investigate effects of population density on food limitation, an important link in understanding how crowding functions to regulate populations. We quantified three components of foraging behavior (prey attack rate, foraging speed, and relative use of morphologically constrained attack maneuvers) for male Black-throated Blue Warblers (*Dendroica caerulescens*) breeding under experimentally manipulated density conditions. Building on the previous work showing the density of conspecific neighbors affects territory size, reproductive success, and the time budgets of males (Sillett et al. 2004, Ecology 85: 2467–2477), we further show that density affects male foraging strategies. Although not differing in attack rate or foraging speed, male Black-throated Blue Warblers on territories with reduced neighbor densities used energetically expensive aerial attack maneuvers significantly less frequently than males in control (high-density) territories during both the incubation period and when provisioning nestlings and fledglings. We conclude that males altered their foraging behavior to compensate for density-related reductions in time available for foraging and that population density may constrain the time available for foraging.

SINOPSIS. **La densidad poblacional afecta la conducta de forrajeo de individuos de *Dendroica caerulescens* durante la temporada reproductiva**
La conducta de forrajeo muchas veces refleja la disponibilidad de alimentos, un recurso que puede limitar la capacidad reproductiva con el aumento en el número de individuos. El medir la conducta de forrajeo, puede proveer de una forma de investigar el efecto de la limitación de alimentos en la dencidad poblacional, enlace importante para entender como el acinamiento funciona para regular una población. Cuantificamos tres componentes de la conducta de forrajeo (tasa de ataque de la presa, velocidad de forrajeo, y uso relativo de maniobras de ataque con respecto a restricciones morfológicas) para machos de *Dendroica caerulescens* reproduciéndose bajo densidades manipuladas experimentalmente. Utilizando como base trabajos que señalan que la densidad conespecífica vecinal afecta el tamaño del territorio, el éxito reproductivo y el presupuesto utilizado por los machos (Sillett et al. 2004, Ecology 85:2467-2477) demostramos que la densidad afecta además la estrategia de forrajeo de los machos. Aunque no hay diferencia en la tasa de ataque o velocidad de forrajeo, machos en territorios con pocos vecinos, utilizaron maniobras de forrajeo energéticamente más costosas y con una frecuencia significativamente menos costosa que el grupo control (áreas con alta densidad), tanto durante la fase de incubación como la de crianza de pichones. Concluimos que los machos alteran su conducta de forrajeo para compensar por la reducción en la densidad de individuos y en el tiempo disponible para forrajear, y que la densidad de la población puede limitar el tiempo disponible para forrajear.

Key words: attack maneuver, attack rate, competition, crowding, *Dendroica caerulescens,* food limitation, foraging speed, population density, crowding, competition, food limitation

Competition for limited resources, such as food, is thought to drive agonistic interactions among conspecific individuals as population density (i.e., crowding) increases (Rodenhouse et al. 1997, Newton 1998). Food often limits breeding productivity (Martin 1987, Newton 1998), but the importance of food limitation

as a mechanism by which crowding affects avian reproductive success remains little known. Although experimental work has demonstrated that conspecific density negatively affects various components of reproductive success (Alatalo and Lundberg 1984, Torok and Toth 1988, Dhondt et al. 1992, Both 1998), few studies have revealed a causal link between intraspecific crowding and resource competition (Both and Visser 2000, Sillett et al. 2004). Crowding could lead to increased food limitation by reducing territory

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size and hence food availability (e.g., absolute amount of food or amount of food per unit of leaf or twig area), by increasing time spent in agonistic interactions and thereby reducing time available for foraging, or both. Consequently, effects of crowding may be manifest in the foraging behavior of individuals. Understanding how foraging strategies vary with population density may thus provide important insights into how agonistic interactions between individuals influence food availability and foraging behavior and, ultimately, contribute to population regulation.

Several measures of avian foraging behavior vary with prey abundance in predictable ways and, therefore, can serve as indices of food availability (Hutto 1990, Lovette and Holmes 1995). Attack rate (number of attacks/unit time), for example, reveals how often a foraging bird encounters prey, and typically increases as prey abundance increases (Hutto 1990, Lovette and Holmes 1995, Johnson 2000). A related variable, foraging speed (number of perch changes/unit time while foraging), reflects foraging effort; by increasing its rate of movement, a bird may search more substrate and potentially increase its prey encounter rate (Robinson and Holmes 1982). Typically, foraging speed and attack rate are positively correlated in arboreal-foraging migrants during the breeding season (Robinson and Holmes 1982).

Foraging behavior may also reflect variation in food availability relative to demand. That is, birds may adjust their foraging behavior to cope with variable constraints on time and energy available for foraging and for other activities such as territory maintenance and seeking mating opportunities. In response to increasing demands on time and energy (e.g., the transition from incubation to provisioning of nestlings), wood-warblers often increase their use of aerial or sally-type attack maneuvers while decreasing their use of glean maneuvers (Martin and Karr 1990, Petit et al. 1990, Dobbs and Martin 1998). Although aerial maneuvers are assumed to be energetically expensive compared to gleaning, this shift to aerial maneuver use is thought to facilitate an increase in food intake per unit time or energy, or an increase in the range of food-types available (Rudolph 1982, Dobbs and Martin 1998).

Recent experimental work (Sillett et al. 2004) demonstrated that crowding during the breeding season is an important mechanism regulating the abundance of Black-throated Blue Warblers (*Dendroica caerulescens*), a Nearctic-Neotropical migrant songbird. When neighbor density was experimentally reduced, pairs had larger territories and fledged more young per territory than pairs in naturally high (control) density areas. Over the 1997–1999 study, effects of the density reduction treatment were strongest in 1997, an El Niño year, when environmental conditions were least favorable for breeding (e.g., lower than average daily temperatures early in the season and lower than average food availability). Because poor environmental conditions appeared to amplify the effects of crowding (Sillett et al. 2004), conditions in 1997 provided an ideal opportunity to examine how neighbor density might affect the foraging behavior of individual males. Here we present the results of that study.

We quantified the attack rates and foraging speeds of male Black-throated Blue Warblers and also examined the use of different foraging maneuvers by males on territories in control and reduced-density treatments. Because attack rate and foraging speed are typically positively correlated with prey abundance, we predicted that, if crowding reduces overall food availability (e.g., by reducing territory size), then males with experimentally reduced neighbor density should search for and attack prey at higher rates than control males in territories at normal densities. Because the use of aerial attack maneuvers is often negatively associated with time available for foraging by wood-warblers, we predicted that, if crowding reduces time available for foraging (e.g., by increasing agonistic interactions), then males with reduced neighbor density should use aerial attack maneuvers less frequently than control males.

METHODS

Study area and species. We conducted field work from May to August 1997 in the Hubbard Brook Experimental Forest, near Woodstock, New Hampshire. Our gridded 150-ha study area was comprised of a 20–25 m tall canopy of mature American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*), and an understory dominated by hobblebush (*Viburnum alnifolium*), striped maple (*A. pensylvanicum*), and beech saplings. This site represents high-quality breeding habitat for Black-throated Blue

Warblers (Holmes et al. 1996), with each pair having four to six contiguous, neighboring conspecific pairs (Sillett et al. 2004). Males of this sexually dichromatic species defend nonoverlapping breeding territories within which females construct nests in understory vegetation and, after egg-laying, incubate an average of four eggs for 12–13 d without male assistance (Holmes et al. 2005). Males and females both provision nestlings for 8–10 d, and provide virtually all food for fledglings during the first week after fledging (Holmes et al. 2005). Black-throated Blue Warblers are completely insectivorous during the breeding season and forage primarily in the lower and middle forest strata, with males foraging higher on average than females (Holmes 1986, Holmes et al. 2005). These Warblers typically move rapidly while foraging, and primarily attack prey located on live foliage by snatching it in continuous or hovering flight or by gleaning while perched (Holmes et al. 2005).

Field methods. We manipulated conspecific neighbor density of Black-throated Blue Warblers as part of a three-year experiment investigating the mechanisms driving density-dependent population regulation (Rodenhouse et al. 2003, Sillett et al. 2004). After pairs settled on territories in late May to early June 1997, we created a reduced-density treatment by removing all conspecific pairs whose territories abutted those of four focal pairs (see Sillett et al. 2004 for additional details). The control treatment consisted of nine focal pairs that experienced the normal neighbor density characteristic of the study area. Control territories were randomly selected and separated from areas where density was reduced by at least one and usually several intervening, occupied territories. Habitat characteristics and the spatial distribution of territories (prior to the density manipulation) were similar between experimental and control territories. Adults on all focal territories were captured, aged as either second year or after second year, and marked with unique combinations of one numbered aluminum leg band and two colored-plastic leg bands to allow individual identification. We found all nests of focal pairs and monitored them every two d to determine nest fate and dates of hatching, fledging, or failure.

For foraging behavior observations, we selected all four males from the reduced-density treatment and randomly selected four males from the control treatment to be focal individuals. A single observer (RCD) conducted behavioral observations (continuous recording, focal animal sampling; Martin and Bateson 1993) of these eight males during the incubation, nestling, and early-fledgling stages from 11 June to 23 July (06:00–13:00 EST). Because fledglings remain on natal territories and are completely dependent on their parents for at least the first week after leaving the nest, we combined observations from the nestling and fledgling periods. We randomized the sampling order of focal males and, whenever possible, sampled each focal male on multiple days within each stage of the nesting cycle.

We collected sequences of foraging data by following an actively foraging focal male within its territory and dictating its behavior into a constantly running microcassette tape recorder. After visually locating a focal male through 8 × 30 binoculars, we waited 30 s before starting data collection to prevent bias associated with conspicuous behaviors (e.g., sally-type attack maneuvers). We classified all prey-attack attempts as either glean, sally-hover, or sally-strike (Remsen and Robinson 1990), and all perch change movements as either hop, short flight (≤1 m), or long flight (>1 m) (following Robinson and Holmes 1982). We ended each foraging sequence when the observer either lost view of the focal bird or the bird began performing a nonforaging behavior such as preening. Whenever possible, we relocated a focal bird lost from view to start a new foraging sequence.

We transcribed tapes using a stopwatch to measure the duration of each foraging sequence. For each foraging sequence, we tallied the number of each type of attack and perch change movement observed, and calculated rates of attacks and movements per minute. After discarding foraging sequences <20 s in duration (following Robinson and Holmes 1982) and summing remaining foraging sequences within each day to yield one observation per individual per day, we collected 88.2 min (5290 s) of foraging behavior data, including 424 prey attacks and 2470 perch change movements, for four control and four reduced-density male Black-throated Blue Warblers. Total foraging observation time was less for control males (1850 s) than for reduced-density males (3440 s), due in part to shorter average foraging sequence duration for controls (30.8 s vs. 36.2 s for reduced-density males) and fewer average foraging sequences

collected per day for controls (3.9 vs. 4.7 for reduced-density males).

Statistical analyses. We used linear mixed models to test our predictions regarding effects of neighbor density on attack rates and foraging speed, and the relative use of attack maneuvers by individual males. Models were fit using the restricted maximum likelihood (REML) method. We included neighbor-density treatment, nest stage, and their interaction as fixed effects, and individual male nested within neighbor-density treatment (i.e., male [treatment]) as a random effect in the models. We used SPSS (2002) to examine residuals and calculate all statistics. We combined sally-strike and sally-hover attack maneuvers and, therefore, had two attack maneuver variables: aerial and glean. Although data were transformed when necessary to meet linear model assumptions, results are presented as untransformed means $\pm$ 1 SE.

RESULTS

Contrary to our predictions, density treatment did not affect either the attack rate ($F_{1,6.87} = 0.42$, $P = 0.54$) or foraging speed ($F_{1,6.53} = 0.47$, $P = 0.52$) of male Black-throated Blue Warblers (Fig. 1). Foraging speeds, however, differed significantly among nest stages, with males in both treatments moving at higher rates when feeding nestlings and fledglings (31.7 ± 2.5 movements/min) than when females were incubating eggs (19.8 ± 0.9 movements/min; $F_{1,33.54} = 20.0$, $P < 0.001$; Fig. 1B). Attack rates did not differ among nest stages ($F_{1,32.10} = 1.8$, $P = 0.19$). Interaction terms and individual male effects were not significant.

Neighbor density strongly affected the type of attack maneuver used by male Black-throated Blue Warblers. Males in control territories used aerial attack maneuvers (sally-strike and sally-hover) significantly more than males in the reduced-density treatment ($F_{1,5.06} = 12.8$, $P = 0.016$; Fig. 2). Males in the reduced-density treatment thus gleaned prey from substrates significantly more than males in control territories. The use of attack maneuvers did not differ among nest stages ($F_{1,33.81} = 0.2$, $P = 0.64$), and the interaction term and individual male effects were not significant.
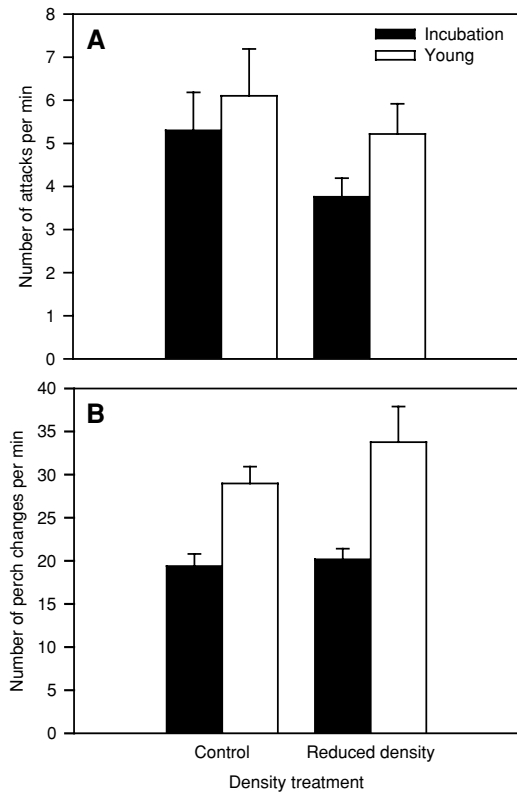

Fig. 1. Density treatment did not affect either attack rate (A) or foraging speed (B) of male Black-throated Blue Warblers. Males in both density treatment groups foraged significantly faster when feeding young than during incubation.

DISCUSSION

Neighbor-density treatment did not affect either attack rates or foraging speed in our study, suggesting that food availability did not differ between the treatment groups. Although contrary to our predictions, the lack of a density-related shift in attack rate or foraging speed is consistent with actual prey abundance measurements from the study site (data in Sillett et al. 2004), with no difference in the mean dry biomass of caterpillars and spiders per 2400 leaves and number of deciduous leaves in the shrub layer between reduced-density and control territories (Sillett et al. 2004). Despite the fact that territories in the reduced-density treatment were significantly larger and thus likely had higher absolute food abundance than control
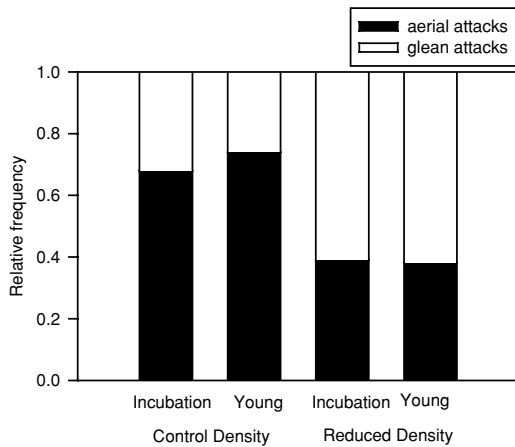
Fig. 2. Male Black-throated Blue Warblers with control (naturally high) neighbor densities used aerial attack maneuvers significantly more frequently than males with experimentally reduced neighbor densities, regardless of nest stage.

territories, prey density was similar in reduced-density and control territories.

Males breeding in areas with experimentally reduced neighbor density adjusted their foraging behavior by reducing their use of aerial attack maneuvers compared to control males. This shift in use of attack maneuvers was consistent with our prediction that reduced-density males would experience relaxed time constraints, and thus use fewer aerial attack maneuvers than control males. Indeed, the decrease in use of aerial maneuvers by reduced-density males coincided with a shift in time budgets, with males in the reduced-density treatment allocating more time to foraging than control males (Sillett et al. 2004). These results suggest that males in areas with a higher density of territories compensated for the reduced time available for foraging by using aerial attack maneuvers more than males in areas with lower densities. In support of this conclusion, previous research has shown that wood-warblers can adjust to increased time or energy constraints by shifting attack maneuver use away from gleaning in favor of sally-type aerial maneuvers (Martin and Karr 1990, Petit et al. 1990, Dobbs and Martin 1998), possibly to increase prey biomass captured per unit time or to increase the range of prey types available. Presumably, there is a cost to frequent use of aerial attack maneuvers that prevents individuals

from favoring the use of aerial maneuvers at high and low neighbor densities.

Males in both treatment groups foraged significantly faster after their eggs hatched than before, apparently reflecting adjustment to increased time-energy demands of provisioning young compared to incubation and not an increase in food availability later in the season. If food availability had been responsible for the increase in foraging speed after hatching, attack rate should have exhibited a concomitant increase, but it did not. Similarly, Lovette and Holmes (1995) showed that male American Redstarts (*Setophaga ruticilla*) at Hubbard Brook also increased their foraging speed, but not their attack rate, at the transition from incubation to provisioning young. This suggests that birds increased their foraging effort to maintain previous prey-encounter rates in the face of increased time or energy constraints.

Parulids appear to respond differently to increased time-energy demands. Male Black-throated Blue Warblers (this study) and male American Redstarts (Lovette and Holmes 1995) increased their foraging speeds when they began to feed nestlings, but did not simultaneously increase their use of aerial attack maneuvers. In contrast, male Prothonotary Warblers (*Protonotaria citrea*) increase their use of aerial attack maneuvers after hatching (Petit et al. 1990, Lyons 2005), but apparently do not significantly change their foraging speed after hatching (Lyons 2005). These patterns emphasize the need to consider multiple variables when quantifying foraging behavior. Indeed, a tradeoff between foraging rates and the use of attack maneuvers could explain why male Black-throated Blue Warblers adjusted their use of attack maneuvers, but not attack rates or foraging speed, in response to the density treatment.

Males in the reduced-density treatment tended to feed nestlings at higher rates and produce heavier fledglings than control males in 1997 (Sillett et al. 2004). If adjustments in the use of attack maneuvers also affected either the type or quality of prey that males searched for and attacked, then nestling provisioning rates could have differed between the density treatment groups without concomitant differences in either foraging speeds or attack rates. For instance, if control males tended to capture smaller or lower-quality prey items as a result of using more aerial attack maneuvers

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than reduced-density males, then control males may have had to spend more time away from the nest per foraging bout to acquire adequate prey loads and, therefore, may have made fewer feeding trips to the nest than reduced-density males. Under this scenario, attack rates and foraging speeds of control and reduced-density males would not necessarily have been different. More information is needed to understand relationships between foraging rates, the use of attack maneuvers, and how those relationships may vary with food availability and time-energy constraints.

Our study demonstrates experimentally that population density affects the foraging behavior of individual birds during the breeding season. This is important for two reasons. First, the positive relationship between neighbor density and the frequency of use of aerial attack maneuvers (this study) occurred in parallel with a negative relationship between neighbor density and time spent foraging (Sillett et al. 2004). Birds experiencing high levels of intraspecific interactions in high-density neighborhoods may therefore compensate for time constraints on foraging by adjusting their prey-attack strategies. Although we do not know if or how density-related shifts in attack maneuver use affected the types of prey acquired, males in the reduced-density treatment spent more time foraging and fledged more young than control males (Sillett et al. 2004). Although our study does not demonstrate competition, considering evidence of food limitation at Hubbard Brook (Rodenhouse and Holmes 1992, Nagy and Holmes 2005) and the relationship between crowding, time spent foraging, and reproductive success (Sillett et al. 2004), our results provide additional insight into the role of resource competition as a mechanism by which crowding influences Black-throated Blue Warbler productivity and abundance. Second, our results show that population density affects foraging strategies of individuals independent of potentially confounding ecological factors (e.g., territory quality). This has important implications for constructing predictions and interpreting results in studies of foraging behavior, especially in nonexperimental studies. Investigators using foraging behavior to evaluate habitat quality, for example, must consider that the effects of intraspecific density may confound effects of overall food availability on foraging behavior.

LITERATURE CITED

ALATALO, R. V., AND A. LUNDBERG. 1984. Density dependence in breeding success of the Pied Flycatcher (*Ficedula hypoleuca*). Journal of Animal Ecology 53: 969–977.

BOTH, C. 1998. Experimental evidence for density dependence of reproduction in Great Tits. Journal of Animal Ecology 67: 677–674.

———, AND M. E. VISSER. 2000. Breeding territory size affects fitness: an experimental study on competition at the individual level. Journal of Animal Ecology 69: 1021–1030.

DHONDT, A. A., B. KEMPENAERS, AND F. ADRIAENSEN. 1992. Density-dependent clutch size caused by habitat heterogeneity. Journal of Animal Ecology 61: 643–648.

DOBBS, R. C., AND T. E. MARTIN. 1998. Variation in foraging behavior among nesting stages of female Red-faced Warblers. Condor 100: 741–745.

HOLMES, R. T. 1986. Foraging patterns of forest birds: male-female differences. Wilson Bulletin 98: 196–213.

———, P. P. MARRA, AND T. W. SHERRY. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. Journal of Animal Ecology 65: 183–195.

———, N. L. RODENHOUSE, AND T. S. SILLETT. 2005. Black-throated Blue Warbler (*Dendroica caerulescens*). In: The birds of North America online (A. Poole, ed.). Cornell Laboratory of Ornithology, Ithaca, NY. Available at: http://bna.birds.cornell.edu/BNA/account/Black-throated_Blue_Warbler (Accessed 21 October 2005).

HUTTO, R. L. 1990. Measuring the availability of resources. Studies in Avian Biology 13: 20–28.

JOHNSON, M. D. 2000. Evaluation of an arthropod sampling technique for measuring food availability for forest insectivorous birds. Journal of Field Ornithology 71: 88–109.

LOVETTE, I. J., AND R. T. HOLMES. 1995. Foraging behavior of American Redstarts in breeding and wintering habitats: implications for relative food availability. Condor 97: 782–791.

LYONS, J. E. 2005. Habitat-specific foraging of Prothonotary Warblers: deducing habitat quality. Condor 107: 41–49.

MARTIN, P., AND P. BATESON. 1993. Measuring behaviour: an introductory guide, 2nd ed. Cambridge University Press, Cambridge, UK.

MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics 18: 453–487.

———, AND J. R. KARR. 1990. Behavioral plasticity of foraging maneuvers of migratory warblers: multiple selection periods for niches? Studies in Avian Biology 13: 353–359.

NAGY, L. R., AND R. T. HOLMES. 2005. Food limits annual fecundity of a migratory songbird: an experimental study. Ecology 86: 675–681.

NEWTON, I. 1998. Population limitation in birds. Academic Press, San Diego, CA.

PETIT, L. J., D. R. PETIT, K. E. PETIT, AND W. J. FLEMING. 1990. Intersexual and temporal variation in foraging ecology of Prothonotary Warblers during the breeding season. Auk 107: 133–145.

REMSEN, J. V., JR., AND S. K. ROBINSON. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Studies in Avian Biology 13: 144–160.

ROBINSON, S. K., AND R. T. HOLMES. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63: 1918–1931.

RODENHOUSE, N. L., AND R. T. HOLMES. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. Ecology 73: 357–372.

———, T. W. SHERRY, AND R. T. HOLMES. 1997. Site-dependent regulation of population size: a new synthesis. Ecology 78: 2025–2042.

———, T. S. SILLETT, P. J. DORAN, AND R. T. HOLMES. 2003. Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. Proceedings of the Royal Society of London B 270: 2105–2110.

RUDOLPH, S. G. 1982. Foraging strategies of American Kestrels during breeding. Ecology 63: 1268–1276.

SILLETT, T. S., N. L. RODENHOUSE, AND R. T. HOLMES. 2004. Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. Ecology 85: 2467–2477.

SPSS. 2002. SPSS 11.5.0 for Windows. SPSS Inc., Chicago, IL.

TOROK, J., AND L. TOTH. 1988. Density dependence in reproduction of the Collared Flycatcher (*Ficedula albicollis*) at high population levels. Journal of Animal Ecology 57: 251–258.