

Experimental fruit removal does not affect territory structure of wintering Hermit Thrushes

David R. Brown^{1,2} and Jennifer A. Long^{1,3}

¹Department of Biological Sciences, Southeastern Louisiana University, Hammond, Louisiana 70402 USA

Received 15 May 2006; accepted 29 August 2006

ABSTRACT. Food is generally considered to be the primary resource structuring winter territories in migrant songbirds, but there is little experimental evidence to support this. In southeastern Louisiana, ripe fruits, consumed opportunistically in the absence of preferred arthropod resources, are a primary food resource for wintering Hermit Thrushes (*Catharus guttatus*). To test the possible role of food in controlling space use during the winter, we reduced fruit availability in the territories of wintering Hermit Thrushes and compared responses of these thrushes to those in control territories where fruit availability was not altered. We found that thrushes did not adjust either territory size or location in response to midwinter reduction of fruit availability. One possible explanation for this lack of response is that sufficient food, including arthropods, was available in thrush territories even after removal of fruit. Another possibility is that the removal of fruit did reduce food levels below the level needed to meet energetic needs, but social constraints on territory structure, dictated by fall settlement spacing and maintained by agonistic interactions, prevented birds from adjusting territories to match food supply later in the season.

SILOPIS. **Remoción experimental de frutas, no afecta la estructura territorial de individuos invernales de *Catharus guttatus***

El alimento es generalmente considerado la fuente principal que estructura los territorios de invierno de aves canoras migratorias. Sin embargo, hay poca evidencia experimental para sostener dicha hipótesis. En el suroeste de Louisiana, en ausencia de los artrópodos de su predilección, la fuente principal de alimentos de individuos invernales del zorzal *Catharus guttatus* lo son frutas. Para poner a pruebas el posible rol del alimento en el control de espacio durante el invierno, se redujo la disponibilidad de frutas en el territorio de los zorzales y comparamos sus respuestas con individuos en territorios controles, en donde no se altero la disponibilidad de frutas. Encontramos que los zorzales no ajustaron el tamaño del territorio o la localización en respuesta a la reducción de frutas. Una posible explicación es que todavía quedaba en los territorios suficiente alimento, incluyendo artrópodos, para cumplir con la demanda energética de las aves. Otra posibilidad es que la remoción de frutas, sí redujo de forma crítica la cantidad de alimento. Sin embargo, los zorzales, ya tarde en la temporada, no pudieron ajustar el tamaño del territorio para cumplir con sus demandas energéticas, por las limitaciones sociales en la estructura del territorio dictado por la magnitud de los espacios otoñales y mantenido por interacciones agresivas entre vecinos.

Key words: *Catharus guttatus*, food reduction, fruit, territoriality, winter

In the absence of breeding requirements, food supply is potentially the principle limiting resource for wintering migratory birds (Sherry et al. 2005). Many landbird species are site tenacious through the wintering period, often defending distinct territories (Rappole and Warner 1980, Greenberg and Salewski 2005). Because of the negative relationship between territory size and food supply during the breeding season

(Smith and Shugart 1987), food supply is generally assumed to be a critical factor controlling the structure of winter territories of migratory birds. Food supply is known to affect the distribution and abundance of wintering migratory landbirds at regional and plot scales (Johnson and Sherry 2001, Borgmann et al. 2004, Kwit et al. 2004), but a similar relationship has not been demonstrated at the scale of individual territories.

Hermit Thrushes (*Catharus guttatus*) winter throughout the southeastern United States and are particularly abundant in southeastern Louisiana where they defend small, largely nonoverlapping territories (Jones and Donovan 1996, Brown et al. 2000). Although wintering Hermit Thrushes are omnivorous, they consume fruit opportunistically as a low preference food during periods of cold weather when the

²Corresponding author. Current address: Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803, USA. Email: dbrown5@lsu.edu

³Current address: Department of Biology, 5751 Murray Hall, University of Maine, Orono, Maine 04469, USA.

availability of arthropods declines (Long and Stouffer 2003, Strong et al. 2005).

We predicted that wintering Hermit Thrushes would adjust territory size, location, and movement patterns in response to changes in the availability of their food supply during midwinter. We tested this by experimentally removing fruit from the territories of wintering Hermit Thrushes and monitoring their use of space relative to a group of control birds. Specifically, we predicted that territory sizes and movement distances of birds in fruit-reduced territories would increase relative to those of control birds. We also predicted that experimental birds would shift their territories after fruit reduction treatment so that locations of post- and premanipulation territories would differ more than for control birds.

METHODS

Our study was conducted in a stand (2.25 km²) of managed loblolly pine (*Pinus taeda*; 16 yrs of age) in Tangipahoa Parish, Louisiana (30°41'N, 90°28'W). This relatively homogeneous stand was characterized by a dense canopy with an average height of 5–7 m. Although loblolly pine was the dominant species, scattered hardwood species and fruiting shrubs such as yaupon (*Ilex vomitoria*) and privet (*Lingustrum* sp.) were also present. The dense understory included trunks and accumulated dead woody material, and vegetated ground cover was sparse. All field work was conducted from January to early February 2000 when yaupon and privet were in peak fruit (Strong et al. 2005).

Our study area had a high density of Hermit Thrushes that maintained distinct, minimally overlapping territories (Brown et al. 2002). We used playback recordings and blanket netting to capture and radio-tag 10 Hermit Thrushes. To avoid direct interaction between individuals, we attempted to capture birds separated by at least one territory (Brown et al. 2000). We banded birds with USGS aluminum and colored-plastic bands, and attached a small radio-transmitter (1.4 g; Wildlife Materials, Inc., Carbondale, IL, USA) using a leg-loop harness. Birds were located by single observer triangulation using two or three bearings. We used ARCVIEW Animal Movements program for home range analyses (Hooge and Eichenlaub 1997).

We randomly assigned each bird to either control or reduction treatment and monitored their movements for 10 days (mean number of locations per individual = 25.6 ± 0.37 [SE]) before initiating treatments. We surveyed pre-manipulation fruit availability in each territory by counting all ripe privet and yaupon fruits along three randomly located 12 m × 2 m transects. Treatments were conducted within a 25-m² area (60% of average territory size; Brown et al. 2000) centered on the pretreatment territory location. Most treatment areas were square, but several were either rectangular or trapezoid to better reflect the shape of territories. For experimental birds we manually removed all fruiting shrubs within each 25-m² territory core. For control birds we removed a similar number of nonfruiting woody plants of similar size from territory cores to control for the permanent structural change and temporary disturbance of removal work within experimental territories. In both experimental and control territories, plants were cut with machetes or chain saws and removed from the treatment area. Following manipulation we monitored the locations of birds for 15–18 days (mean number of locations per individual = 37.2 ± 1.6 [SE]).

To calculate a utilization distribution, we used a fixed-kernel technique with least-squares cross validation to select the smoothing factor (White and Garrott 1990). We compared the changes in territory size (95% utilization distribution) from pre- to postmanipulation and between control and experimental birds. We also determined the percent overlap of the postmanipulation utilization distribution (95%) over the premanipulation utilization distribution. In addition to contour areas, kernel-based utilization distributions have an associated volume based on the density of locations (Millsbaugh and Marzluff 2001). We used these volume estimates to calculate the volume of intersection of postmanipulation utilization distributions over premanipulation utilization distributions. We also calculated pre- to postmanipulation changes in the geometric center of activity and the mean distance of movement between locations. We used SYSTAT to conduct paired *t*-tests that compared pre- and postmanipulation changes between control and experimental birds (Wilkinson 2000). For all descriptive statistics, we report mean ± 1 SE.

RESULTS

Changes in territory size after manipulation for experimental and control groups, as estimated by a 95% utilization distribution, did not differ ($t_9 = 0.48$, $P = 0.67$; Fig. 1). Similarly, there was no difference between treatments in either the extent of overlap of pre- and postmanipulation territories ($70.0 \pm 10.0\%$ for both; $t_9 = -0.43$, $P = 0.67$) or the movement of the center of activity after manipulation ($t_9 = -0.45$, $P = 0.68$). The mean distance between center of activities for the pre- and postmanipulation periods was 16.8 ± 4.1 m for the food-reduced group and 23.8 ± 5.3 m for the control group. There was also no shift in intensity of use as calculated from the utilization distribution volume of intersection ($t_9 = 0.75$, $P = 0.21$). The volume of intersection of utilization distributions for the pre- and post-manipulation periods was $62.0 \pm 7.0\%$ for the food reduction group and $52 \pm 11.3\%$ for the control group. Finally, the average distance between consecutive locations for control and experimental groups did not differ after manipulation ($t_9 = 1.40$,

$P = 0.19$), with mean movement declining by 5.3 ± 3.6 m for experimental birds and 6.5 ± 2.8 m for control birds.

DISCUSSION

We reduced within-territory fruit resources of wintering Hermit Thrushes and found no response in terms of territory size and location. Possible explanations for our results include type-II error, different or flexible diet, and social constraints. First, we may not have detected a response (i.e., type-II error) because birds were not monitored long enough after manipulation. We may have removed enough fruit to affect long-term needs, but availability of arthropods and any undetected, unremoved fruit may have been sufficient to meet the energetic demands of Hermit Thrushes over the two week postmanipulation period. Unfortunately, additional monitoring was not possible because of the limited life-span of the transmitter batteries.

A related explanation is that treatment birds were able to subsist on the fruit remaining in the peripheral 40% of territories that was untreated. If true, treatment birds should have increased activity in these peripheral areas, and this would have resulted in a postmanipulation shift of territory locations and inflation in the size of utilization distributions. Our data did not reveal such a response.

A second possible explanation for the lack of response to food reduction is that sufficient food was available in thrush territories even after removal of fruit. Fruit can be an important component of the diet of Hermit Thrushes wintering in southeastern Louisiana (Strong et al. 2005). However, arthropods are a preferred food resource and were probably available during our study because the mean temperature in Amite, Louisiana (4 km from our study site) for January 2000 was 11.7°C . At that temperature, some arthropods would likely be active and available to foraging thrushes (Avery and Krebs 1984). As a result Hermit Thrushes may have found sufficient food in their territories, in the form of arthropods or remaining fruit, even after fruit removal.

The third possible explanation involves constraints. If we manipulated food to a level biologically important to Hermit Thrushes, then social constraints could have limited behavioral adjustment to changes in food availability.

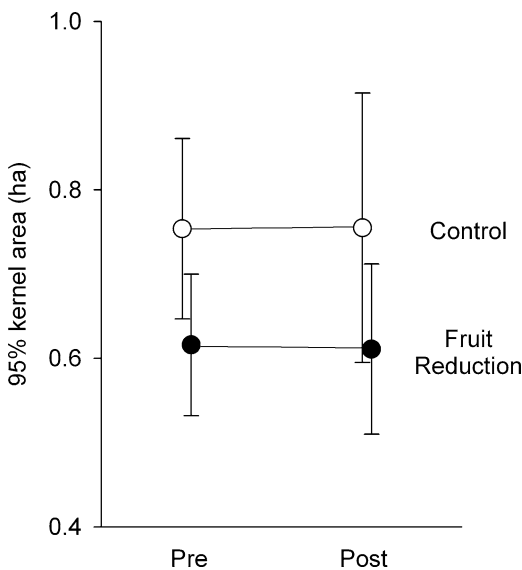


Fig. 1. Territory size of Hermit Thrushes before (pre) and after (post) manipulation. Experimental manipulation entailed reduction of fruit supply by removing fruiting shrubs from the core of each bird's territory. For control birds, we removed similar numbers of nonfruiting shrubs from the core of each bird's territory.

Previous work suggests that agonistic social interactions influence the spacing behavior of wintering Hermit Thrushes in our study area. In the same area used in our study, Brown et al. (2002) found that most male and female Hermit Thrushes defended small (\bar{x} = 0.42 ha), minimally overlapping (\bar{x} = 16%) territories using agonistic vocalizations and displays. The population also included floaters (15% of all individuals) that moved through the territories of other thrushes, possibly seeking vacancies (Brown et al. 2000). Based on Brown et al.'s (2002) results, our study area was classified as high-quality habitat for wintering Hermit Thrushes relative to hardwood forest based on several demographic indices, including physical condition and annual return rates of thrushes. Because Hermit Thrushes occupy high-quality habitats before lower quality habitats during the fall arrival period (Brown et al. 2002), our study area reached a stable density before substantial numbers of birds settled in lower-quality habitat. The combination of small territories, limited territory overlap, frequent agonistic interactions, the presence of floaters, and the incremental selection of habitat during settlement suggest that the population in our study area was at saturation densities with respect to available resources.

Assuming saturation density, our data could be interpreted to suggest that individual territory structure may be inflexible to changes in food supply after the settlement period (Arvidsson et al. 1997). In a densely packed area with territorial and floater birds, maintaining a territory, even with depleted food resources, may outweigh the risk of abandoning a territory and attempting to establish a new one. Even in conditions of depleted food resources, intense intraspecific competition, or at least the residual spacing from competition that occurred during the arrival period, may constrain birds from adjusting the size and location of their territories. However, such a direct link remains to be demonstrated. To address this hypothesis, further study is needed during the fall arrival period when agonistic interactions and exploratory movements are more frequent (Brown et al. 2000, Price 1981). Although the benefits of early arrival by migratory birds on their breeding grounds are well documented (Perrins 1970, Møller 1994, Lozano et al. 1996, Smith and Moore 2003), the consequences of early arrival

during the winter season are poorly understood. Early arrival on wintering grounds is thought to improve dominance rank through priority effects (Ketterson and Nolan 1976, Snell-Rood and Cristol 2005; but see Marra 2000), but no other effects have been studied. Populations of migratory birds are limited, in part, by ecological factors on the wintering grounds, including food availability (Brown and Sherry 2006) and dominance-mediated habitat occupancy (Marra et al. 1998, Norris et al. 2004). Thus, it would be worthwhile to consider the behavioral, physiological, and population consequences of different arrival times on the wintering grounds.

ACKNOWLEDGMENTS

A. Parsons and C. Strong assisted with field work, and two anonymous reviewers provided valuable comments that improved the quality of the manuscript. Financial support came from a Louisiana Education Quality Support Fund grant to P. Stouffer. Weyerhaeuser Company gave us permission to work on their property and provided logistical support during fruit removal. All work was conducted under appropriate USGS permits for banding and use of auxiliary markers.

LITERATURE CITED

- ARVIDSSON, B., C. ASKENMO, AND R. NEERGAARD. 1997. Food supply for settling male Rock Pipits affects territory size. *Animal Behaviour* 54:67–72.
- AVERY, M. I., AND J. R. KREBS. 1984. Temperature and foraging success of Great Tits *Parus major* hunting for spiders. *Ibis* 126: 33–38.
- BORGMANN, K. L., S. F. PEARSON, D. J. LEVEY, AND C. H. GREENBERG. 2004. Wintering Yellow-rumped Warblers (*Dendroica coronata*) track manipulated abundance of *Myrica cerifera* fruits. *Auk* 121:74–87.
- BROWN, D. R., AND T. W. SHERRY. 2006. Food supply controls body condition of a migrant bird wintering in the tropics. *Oecologia* 149: 22–32.
- , P. C. STOFFER, AND C. M. STRONG. 2000. Movement and territoriality of wintering Hermit Thrushes in southeastern Louisiana. *Wilson Bulletin* 112: 347–353.
- , C. M. STRONG, AND P. C. STOFFER. 2002. Demographic effects of habitat selection by Hermit Thrushes wintering in a pine plantation landscape. *Journal of Wildlife Management* 66: 407–416.
- GREENBERG, R., AND V. SALEWSKI. 2005. Ecological correlates of wintering social systems in new world and old world migratory passerines. In: *Birds of two worlds* (R. Greenberg, and P. P. Marra, eds.), pp. 336–358. Johns Hopkins University Press, Baltimore, MD.
- HOOG, P. N., AND B. EICHENLAUB. 1997. Animal movement extension 2.0. Alaska Science Center—biological science office, U.S. Geological Survey, Anchorage, AK.

- JOHNSON, M. D., AND T. W. SHERRY. 2001. Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. *Journal of Animal Ecology* 70: 546–560.
- JONES, P. W., AND T. M. DONOVAN. 1996. Hermit Thrush (*Catharus guttatus*). In: *The birds of North America*. (A. Poole, and F. Gill, eds.), pp. 1–28. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists Union, Washington, D.C.
- KETTERSON, E. D., AND V. NOLAN JR. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*). *Ecology* 57:679–693.
- KWIT, C. J., D. J. LEVEY, C. H. GREENBERG, S. F. PEARSON, J. P. MCCARTY, S. SARGENT, AND R. L. MUMME. 2004. Fruit abundance and local distribution of wintering Hermit Thrush (*Catharus guttatus*) and Yellow-rumped Warblers (*Dendroica coronata*) in South Carolina. *Auk* 121:46–57.
- LONG, J. A., AND P. C. STOUFFER. 2003. Diet and preparation for spring migration in captive Hermit Thrushes (*Catharus guttatus*). *Auk* 120: 323–330.
- LOZANO, G. A., S. PERREULT, AND R. E. LEMON. 1996. Age, arrival date, and reproductive success of male American Redstarts *Setophaga ruticilla*. *Journal of Avian Biology* 27:164–170.
- MARRA, P. P. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behavioral Ecology* 11: 299–308.
- MARRA, P. P., K. A. HOBSON, AND R. T. HOLMES. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886.
- MILLSPAUGH, J. J., AND J. M. MARZLUFF. 2001. *Radio tracking and animal populations*. Academic Press, San Diego, CA.
- MØLLER, A. P. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. *Behavioral Ecology and Sociobiology* 35: 115–122.
- NORRIS, D. R., P. P. MARRA, T. K. KYSER, T. W. SHERRY, AND L. M. RATCLIFFE. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London B* 271:59–64.
- PERRINS, C. M. 1970. The timing of birds' breeding season. *Ibis* 112:242–255.
- PRICE, T. 1981. The ecology of the Greenish Warbler *Phylloscopus trochiloides* in its winter quarters. *Ibis* 123:131–143.
- RAPPOLE, J., AND D. WARNER. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. In: *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation* (A. Keast, and E. S. Morton, eds.), pp. 353–393. Smithsonian Institution Press, Washington, D.C.
- SHERRY, T. W., M. D. JOHNSON, AND A. M. STRONG. 2005. Does winter food limit populations of migratory birds? In: *Birds of two worlds* (R. Greenberg, and P. P. Marra, eds.), pp. 414–425. Johns Hopkins University Press, Baltimore, MD.
- SMITH, R. J., AND F. R. MOORE. 2003. Arrival fat and reproductive performance in a long distance passerine migrant. *Oecologia* 134:325–331.
- SMITH, T. M., AND H. H. SHUGART. 1987. Territory size variation in the Ovenbird: the role of habitat structure. *Ecology* 63: 695–704.
- SNELL-ROOD, E. C., AND D. A. CRISTOL. 2005. Prior residence influences contest outcome in flocks of nonbreeding birds. *Ethology* 111:441–454.
- STRONG, C. M., D. R. BROWN, AND P. C. STOUFFER. 2005. Frugivory by wintering Hermit Thrush in Louisiana. *Southeastern Naturalist* 4: 627–638.
- WHITE, G. C., AND R. A. GARROTT. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, San Diego, CA.
- WILKINSON, L. 2000. SYSTAT 10.0. SPSS, Chicago, IL.