

## PRIOR BREEDING SUCCESS AFFECTS RETURN RATES OF TERRITORIAL MALE OVENBIRDS

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**Abstract.** I examined the hypothesis that male Ovenbirds (*Seiurus aurocapillus*) make breeding dispersal decisions based on prior breeding experience at a site. I determined the reproductive success of color-banded male Ovenbirds at sites in fragmented and unfragmented landscapes in Missouri from 1992–1995. I documented which individuals returned and I recorded their reproductive success upon return as well as the success of birds new to each plot. I obtained similar results in both landscapes. Males with different histories of reproductive success returned at different rates. Only 2 of 22 males that were paired but failed to raise young returned in the following year, whereas the return rates of unpaired males (41%,  $n = 37$ ) and males that successfully raised young (54%,  $n = 57$ ) did not differ significantly ( $P = 0.19$ ). The patterns were more consistent with the hypothesis that return rates were due to decisions about dispersal rather than difference in survival of individuals in these groups.

**Key words:** *breeding dispersal, forest fragmentation, Ovenbirds, reproductive success, return rate, Seiurus aurocapillus.*

### El Éxito Reproductivo Previo Afecta Índices de Regreso de Machos Territoriales de *Seiurus aurocapillus*

**Resumen.** Examiné la hipótesis de que individuos de *Seiurus aurocapillus* hacen decisiones de dispersión reproductiva basadas en las experiencias reproductivas previas en un sitio. Determiné el éxito reproductivo de machos con anillos de color en lugares en terrenos fragmentados y no fragmentados de Missouri entre 1992 y 1995. Documenté cuáles individuos regresaron y su éxito reproductivo al regresar, y también el éxito de pájaros nuevos en cada sitio. Obtuve resultados semejantes en ambos paisajes. Los machos con historias de éxito reproductivo diferentes presentaron índices de regreso diferentes. Solamente 2 de 22 machos apareados que no produjeron cría volvieron al año siguiente, mientras que los índices de regreso de machos no apareados (41%,  $n = 37$ ) y de los machos que produjeron crías exitosamente (54%,  $n = 57$ ) no difirieron significativamente ( $P = 0.19$ ). Los patrones concuerdan más con la hipótesis de que los índices de regreso se debieron a las decisiones de dispersión y no a la diferencia de supervivencia de individuos en estos grupos.

## INTRODUCTION

Animals that breed more than once in their lifetime have the option of subsequently breeding in the same location or dispersing to a new location. Adult breeding dispersal affects both the ecology and genetics of populations (Johnson and Gaines 1990). Breeding dispersal of migratory birds has received attention for many years (Hinde 1956), but questions about the ultimate causes of this behavior remain (Greenwood and Harvey 1982). Individuals of many species show greater return rates or shorter dispersal distances following successful breeding in the previous year (Drilling and Thompson 1988, Bo-

llinger and Gavin 1989, Haas 1998). Response to reproductive failure may vary among sex or age classes with females and younger individuals generally being more likely to disperse (Payne and Payne 1993).

Addressing ultimate causation requires knowledge of the reproductive success of returning versus nonreturning individuals. This information has been obtained to varying degrees in a few studies (Beletsky and Orians 1987, Drilling and Thompson 1988, Part and Gustafsson 1989, Payne and Payne 1993), but because dispersal distances are often large, it is difficult to determine the fate of individuals that fail to return. One study has experimentally induced failure and concluded that this caused lower return rates (Haas 1998).

In the course of an intensive study of Ovenbird (*Seiurus aurocapillus*) populations at sites in fragmented and unfragmented landscapes

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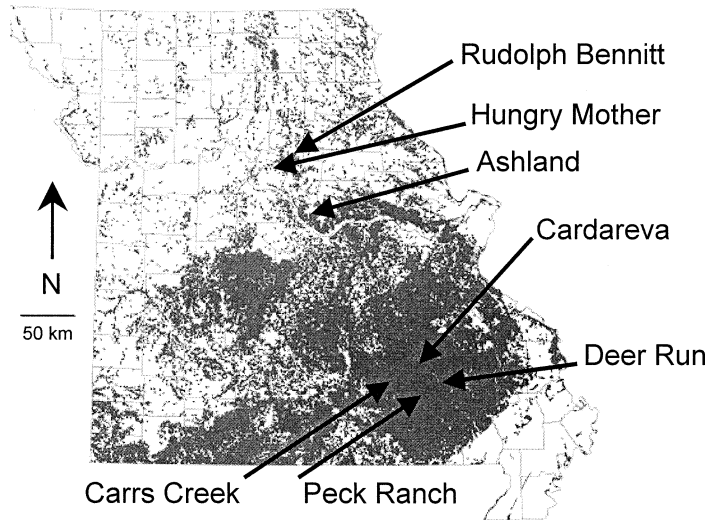


FIGURE 1. Location of study sites and forest cover (shaded) in Missouri. Sites in the fragmented landscape included Ashland, Hungry Mother and Rudolph Bennitt. Sites in the unfragmented landscape included Cardareva, Carrs Creek, Deer Run and Peck Ranch.

(Porneluzi and Faaborg 1999), I determined the reproductive success of color-marked males on permanent plots over several years, documented whether they returned in the following year, and recorded their subsequent reproductive success along with that of birds new to the plot. Categories of reproductive success included unpaired males, males paired but unsuccessful at raising young, and males paired and successfully raising at least one young.

In this paper, I examine whether male return rates differed with landscape or among the three categories of reproductive success. To evaluate the adaptive benefit of returning, I examine the subsequent success of males upon return, and also ask whether territories with unsuccessful individuals in one year are likely to contain unsuccessful individuals in the following year. Few studies have addressed whether returning unpaired males choose the same territory and are successful in the following year. If females choose mates based on some aspect of the territory, returning unpaired males should disperse, whereas if female choice is less dependent on territory attributes (Morris and Lemon 1988), there may be no advantage to dispersal by unpaired males.

## METHODS

### STUDY AREA

I studied Ovenbird demography at seven sites with similar vegetation characteristics in two

contrasting landscapes. All sites were predominantly mature (>40 years) oak-hickory (*Quercus-Carya*) forests within which I concentrated efforts at one randomly selected plot per site. Nonforest habitat in both landscapes consisted mostly of cool-season pasture and row crops.

Three sites were in a highly fragmented landscape in Boone, Howard, and Randolph Counties in central Missouri (Fig. 1). These counties have 24%, 18%, and 19% forest cover respectively (Giessman et al. 1986). I refer to these as sites within the fragmented landscape. The years of study, plot area, forest area, and percent forest within 10 km for each study site appear in Table 1.

Four sites were in an unfragmented landscape in Carter, Reynolds, and Shannon Counties in the southeast Missouri Ozark Mountains. These represent three of the most heavily forested counties in Missouri with 87%, 86% and 83% forest cover respectively (Giessman et al. 1986). These sites were situated in the center of 1.8 million ha of continuous forest.

### TERRITORY IDENTIFICATION

My field assistants and I censused territories at each site every three to four days throughout the breeding season (1 May–15 July) using standard spot-mapping methods (Anonymous 1970). During mapping, we noted the location, identity, and behavior of the birds on enlarged topographic

TABLE 1. Characteristics of sites used to study breeding success and return rates of Ovenbirds in two landscapes in Missouri.

Site	Years of study	Plot area (ha)	Continuous forest area (ha)	% Forest within 10 km
Fragmented				
Ashland	1993–1995	81	4060	42
Hungry Mother	1993–1995	56	2490	33
Rudolph Bennitt	1993–1995	87	2020	37
Unfragmented				
Cardareva	1992–1995	36	1.8 million	92
Carrs Creek	1993–1995	34	1.8 million	92
Deer Run	1992–1995	44	1.8 million	92
Peck Ranch	1992–1995	40	1.8 million	92

maps (scale 1:4270). We used 150-m-interval gridlines marked in the forest and on the maps as an aid to orientation. We recorded observations of simultaneous singing to help us determine the number of birds and the locations of territory boundaries. We captured males by playing a tape-recorded Ovenbird song near a decoy situated inside the 90° angle of two 12-m mist nets. Once captured, each male received a numbered U.S. Fish and Wildlife Service aluminum band and two colored bands in a unique combination that allowed visual identification of individuals. We spot-mapped from 27 to 48 territories and banded 49% to 90% of the territorial males each year (Table 2). We assigned a territory to an unbanded male only if we repeatedly observed an unbanded male singing in that location throughout the breeding season. Although not all males on a site were color banded, we could confidently distinguish unbanded birds as distinct individuals within a breeding season be-

cause of our attention to simultaneous observations of neighboring individuals and because an unbanded bird's territory was generally surrounded by those of banded birds.

REPRODUCTIVE SUCCESS AND RETURN RATES

My primary goal was to determine if males were successful at raising young. I classified males as paired if they were seen or heard interacting with a female, carrying food or nest material, or defending a nest or fledglings. Because Ovenbirds are monomorphic, we identified birds as females if they were observed simultaneously with a singing male and did not countersing or interact aggressively. Each time we encountered a male during spot-mapping, we followed that individual for up to 60 min, until we found a nest or observed the male feeding or defending fledglings. If no evidence of breeding success was observed, we specifically returned to search

TABLE 2. Number of banded and unbanded territorial male Ovenbirds monitored for breeding success and return behavior per site per year in two Missouri landscapes.

Site	No. of banded/unbanded males				Total (% banded)
	1992	1993	1994	1995	
Fragmented					
Ashland		3/6	3/4	3/4	9/14 (39)
Hungry Mother		4/6	6/2	6/5	16/13 (55)
Rudolph Bennitt		8/8	11/9	5/14	24/31 (44)
Unfragmented					
Cardareva	11/1	7/2	8/1	4/2	30/6 (83)
Carrs Creek		4/1	7/4	2/4	13/9 (59)
Deer Run	11/2	9/2	10/0	8/4	38/8 (83)
Peck Ranch	5/0	4/1	3/3	5/2	17/6 (74)
Total	27/3	39/26	48/23	33/35	147/87 (63)

those territories on subsequent visits. As a result, territories of unpaired males were visited more frequently and for a longer duration than territories of successful males. We were generally able to visit each territory (as identified by capturing males and previous censuses) during each census so that an accurate determination of pairing success could be made.

We mapped the locations of nests and monitored them every 3 to 4 days. When we suspected a nest had fledged, we verified this by locating the fledglings. We inspected all nests for the presence of Brown-headed Cowbird (*Molothrus ater*) eggs or nestlings and were alert to the distinctive begging chip emitted by fledgling cowbirds (Lowther 1993). Ovenbirds defend their young aggressively, especially before the young can fly (Hann 1937), making detection of family groups relatively easy. My assistants and I "pished" and chipped to elicit defensive behavior from adults and then visually verified the presence of fledglings. I classified the pair as successful if we observed them defending fledglings (either Ovenbirds or cowbirds). Ovenbirds do not appear to be able to distinguish young cowbirds from their own offspring, as they will continue to raise broods containing only cowbirds. Therefore, raising fledglings of either species would probably be perceived as success by the returning male.

I was unable to test whether males raising a greater number of offspring were more likely to return in the following year. I was not able to accurately count the number of fledglings produced by each pair. Ovenbirds are known to raise only one brood per year (Van Horn and Donovan 1994), and I observed no evidence of males attending more than one brood.

In each year following the first, I determined which males returned to the study sites and their reproductive success. I periodically used Ovenbird song playbacks on and adjacent to the territories to attract and identify certain males. No males returned in year three without also returning in year two.

#### STATISTICAL ANALYSES

My primary objective was to determine if return rates differed among males in three categories of reproductive success: unpaired males, males that were paired but failed to raise young, and males that raised young. I used  $G$ -tests to compare the rates of return in the different categories

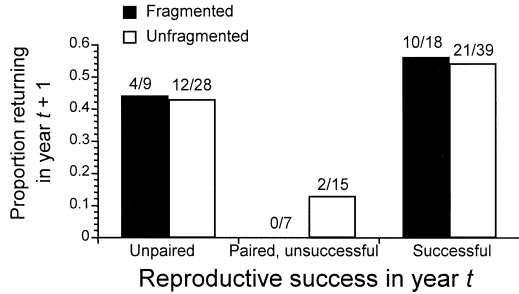


FIGURE 2. Proportion of male Ovenbirds returning in year  $t + 1$ , grouped by their reproductive success in year  $t$ , for fragmented and unfragmented landscapes in Missouri. Males settling more than 200 m from their previous territory would not have been observed and were classified as not returning.

(Zar 1984) with significance accepted at  $P < 0.05$ .

#### RESULTS

Return rates varied among the three classes of reproductive success ( $G_2 = 14.3$ ,  $P < 0.001$ , Fig. 2). Males that were paired but failed to raise young rarely returned in the following year (2 of 22). Return rates of unpaired males (41%,  $n = 37$ ) and males that raised young (54%,  $n = 57$ ) did not differ ( $G_1 = 1.7$ ,  $P = 0.19$ ). The pattern of return among reproductive success classes appeared to be the same in both fragmented and unfragmented landscapes (Fig. 2).

Upon return, males settled on or very near their previous territory. Of 47 returning males, 30 (64%) had territories with  $>50\%$  overlap and 12 (26%) were adjacent to or overlapped  $<50\%$  with the territory of the previous year. The remaining 5 (10%) were not adjacent to the territory of the previous year, but were separated by  $<200$  m. Males settling more than 200 m from their previous territory would not have been observed and were classified as not returning.

Of the 30 males returning after a successful previous year, 24 paired and 20 (83%) of these successfully raised young again. This was a significantly greater rate of success than observed among the remaining paired males (59%,  $n = 129$ ,  $G_1 = 5.7$ ,  $P = 0.02$ ), whose history was unknown.

The distribution of territory overlap did not differ between paired and unpaired males ( $G_2 = 1.0$ ,  $P = 0.60$ ). Unpaired males also returned to essentially the same location occupied in the previous year. Upon return, unpaired males

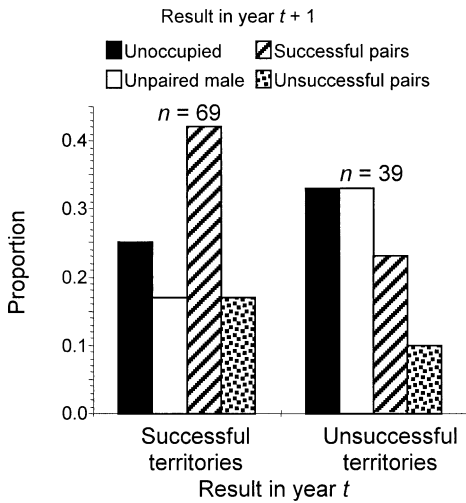


FIGURE 3. Proportion of Ovenbird territories that were unoccupied, held an unpaired male, or held successful or unsuccessful males in year  $t + 1$ , grouped by success of the birds in that territory in year  $t$ .

achieved a rate of pairing success (73%,  $n = 15$ ) that did not differ from the pairing success of previously successful males (80%,  $n = 30$ ,  $G_1 = 0.3$ ,  $P > 0.5$ ). Similarly, the percentage of previously unpaired males that raised young upon return (53%,  $n = 15$ ) did not differ from the percentage of previously successful males raising young upon return (67%,  $n = 30$ ,  $G_1 = 0.7$ ,  $P = 0.39$ ).

Territories that held successful pairs did not differ significantly from territories that held unsuccessful pairs in their fate in the following year ( $G_3 = 6.5$ ,  $P = 0.09$ , Fig. 3). Territories that were successful tended to be more likely to hold successful pairs again in the following year. This appeared to be driven by a greater tendency for territories that held unsuccessful pairs in the previous year to be unoccupied or to be settled by unpaired males in the following year (Fig. 3). Territories that held unsuccessful pairs one year were not more likely to hold unsuccessful pairs again in the following year.

DISCUSSION

Return behavior of male Ovenbirds depended on nest fate during the previous breeding season. Few males with failed nests returned within 200 m, whereas most unpaired males and successful males returned to the same location they had used in the previous year. Males may benefit from prior experience at that location. Benefits

may include relative ease of territory acquisition due to site dominance (Krebs 1982), reduced cost of territory establishment and defense due to neighbor recognition (Falls 1982, Godard 1991), or increased efficiency of resource use resulting from prior learning at that location. It appears that unpaired males also gain from returning to the same location in the following year. Upon return, unpaired males achieved a rate of pairing success and reproductive success that was similar to that of returning successful males. Males with failed nests forgo these benefits and disperse, possibly because failure in one year increases the probability of failure in the following year. The pattern of return among reproductive success classes was the same in both fragmented and unfragmented landscapes. Overall return rates did not differ between sites in the two landscapes either (Porneluzi and Faaborg 1999).

Two hypotheses could explain the variation in return rate among territorial male Ovenbirds with different histories of reproductive success (unpaired, paired but unsuccessful, and successful). One is that return-rate differences reflected differences in survival. Males with failed nests may have had lower survival than unpaired males and successful males.

It is not clear whether males with failed nests would experience lower survival than unpaired males and successful males. Male Ovenbirds provide the majority of food when the nestlings first hatch, but are not involved in nest building or incubation (Hann 1937). Males with failed nests may have to endure the greater risks and costs of repeated re-nesting. These costs would be greater if the nests failed after hatching. However, successful males have the additional cost of caring for fledged young and were not necessarily successful in their first nest attempt. Askenmo (1979) concluded that the costs of breeding decreased survival among male Pied Flycatchers (*Ficedula hypoleuca*) with experimentally enlarged broods. Even if the risks and costs of several failed nest attempts are greater than raising young, it seems unlikely that they are of sufficient magnitude to explain a return rate of <10% among unsuccessful male Ovenbirds. Furthermore, if survival was reduced by nesting attempts to this extent, much higher survival of unpaired males than successful males would also have been expected. However, unpaired males expend considerable energy in ter-

ritory defense and mate attraction throughout the entire season. They may also be younger or of lesser quality than paired males.

The second hypothesis is that surviving males decided whether to return to a site based on their experience at that site. The information available to males with failed nests was that even upon acquiring a mate, they were unsuccessful at raising a brood at that site. Therefore, those males should disperse. Successful and unpaired males returned to the same location rather than dispersing to a location with unknown history. In support of this hypothesis, the observed return rate of unpaired and successful male Ovenbirds (48%) was similar to estimates of annual survival for this species from this and other studies (60%; Faaborg and Arendt 1995, Porneluzi and Faaborg 1999). It appears that most of the surviving individuals with these two categories of reproductive history returned. Bayne and Hobson (2001) found a similar difference in behavior between successful and unsuccessful male Ovenbirds. They found that in the postfledging period males that failed to breed moved more extensively than successful breeders. These authors suggest that unsuccessful breeders may have been searching to find new territories for future breeding seasons, but they were unable to distinguish unpaired males from paired, unsuccessful males.

Many other studies have observed greater fidelity to a site among birds previously successful at that site (e.g., Greenwood and Harvey 1982, Drilling and Thompson 1988, Bollinger and Gavin 1989). In most of these, nest predation was thought to be the primary cause of reproductive failure, as it was in my study areas (Porneluzi and Faaborg 1999). If this is the case, then the behavioral decision of whether to return to a site based on an individual's history of breeding success may be a general mechanism to avoid nest predation. This implies that individuals settling in a location where nest predation occurred in the previous year are more likely to experience nest predation than individuals settling in a location where nest predation did not occur. The dominant nest predators in this study were American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), raccoon (*Procyon lotor*), and opossum (*Didelphis virginiana*, Porneluzi 1996), all of which frequently occupy the same area for several consecutive years and consistently forage in areas where they have previously been success-

ful. Therefore, an Ovenbird territory that experiences predation in one year may be more likely to experience predation in the following year.

Between-year consistency of locations in breeding performance has been documented (Blancher and Robertson 1985, Beletsky and Orians 1987). However, my data on consistency of failure in Ovenbirds are difficult to interpret. In any year, a given location may be unoccupied, settled by an unpaired male, or settled by a pair that may or may not be successful. Because nesting was not attempted (territories were either unoccupied or occupied by unpaired males) on two-thirds of the locations that had held unsuccessful pairs in the previous year, I was unable to assess whether new individuals settling at these locations were more likely to fail. The greater tendency for territories which held unsuccessful pairs in one year to be unoccupied or to be settled by unpaired males in the following year may indicate that neighboring male and female Ovenbirds also select sites using breeding information from the previous season and avoid settling in these locations. Several studies have concluded that birds may monitor the reproductive performance of neighbors (Nolan 1978, Beletsky and Orians 1987, Bollinger and Gavin 1989).

While these patterns of return and subsequent reproductive success lend support to the hypothesis that males choose to return based on prior experience, experimental testing is necessary to more confidently establish the cause of these patterns and the potential for adaptive benefits (Haas 1998). Our understanding of Ovenbird biology would also greatly benefit from knowledge of female return in response to reproductive failure.

Very few studies have examined return rates of unpaired males. This may be either because unpaired males are uncommon or nonterritorial in some species, or because unpaired males have been overlooked or lumped with unsuccessful males. One study, of unpaired male Collared Flycatchers (*Ficedula albicollis*), found them to disperse greater distances than paired males, but unpaired males were uncommon in that study (five individuals, Part and Gustafsson 1989).

My results have implications for studies that attempt to estimate survival of breeding birds. Studies that estimate survival must assume that individuals that never return to a site are dead (Pollock et al. 1990, Martin et al. 1995). Per-

manent dispersal of individuals that fail to reproduce will cause researchers to underestimate survivorship. An analysis of survivorship estimates by reproductive success category may provide a clue that one category of individuals is more likely to disperse.

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#### LITERATURE CITED

- ANONYMOUS. 1970. Recommendations for an international standard for a mapping method in bird census work. *Audubon Field Notes* 24:723-726.
- ASKENMO, C. 1979. Reproductive effort and return rate of male Pied Flycatchers. *American Naturalist* 114:748-753.
- BAYNE, E. M., AND K. A. HOBSON. 2001. Movement patterns of adult male Ovenbirds during the post-fledging period in fragmented and forested boreal landscapes. *Condor* 103:343-351.
- BELETSKY, L. D., AND G. H. ORIANS. 1987. Territoriality among male Red-winged Blackbirds. *Behavioral Ecology and Sociobiology* 20:21-34.
- BLANCHER, P. J., AND R. J. ROBERTSON. 1985. Site consistency in kingbird breeding performance: implications for site fidelity. *Journal of Animal Ecology* 54:1017-1027.
- BOLLINGER, E. K., AND T. A. GAVIN. 1989. The effects of site quality on breeding-site fidelity in Bobolinks. *Auk* 106:584-594.
- DRILLING, N. E., AND C. F. THOMPSON. 1988. Natal and breeding dispersal in House Wrens (*Troglodytes aedon*). *Auk* 105:480-491.
- FAABORG, J., AND W. J. ARENDT. 1995. Survival rates of Puerto Rican birds: are islands really that different? *Auk* 112:503-507.
- FALLS, J. B. 1982. Individual recognition by sounds in birds, p. 237-310. *In* D. E. Kroodsma and E. H. Miller [EDS.], *Acoustic communication in birds*. Vol. 2. Academic Press, New York.
- GIESSMAN, N. F., T. W. BARNEY, T. L. HAITHCOAT, J. W. MYERS, AND R. MASSENGALE. 1986. Distribution of forestland in Missouri. *Transactions of the Missouri Academy of Science* 20:5-20.
- GODARD, R. 1991. Long-term memory of individual neighbours in a migratory songbird. *Nature* 350:228-229.
- 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.
- HANN, H. W. 1937. Life history of the Ovenbird in southern Michigan. *Wilson Bulletin* 181:145-236.
- HINDE, R. A. 1956. The biological significance of the territories of birds. *Ibis* 98:340-369.
- JOHNSON, M. L., AND M. S. GAINES. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics* 21:449-480.
- KREBS, J. R. 1982. Territorial defense in the Great Tit (*Parus major*): do residents always win? *Behavioral Ecology and Sociobiology* 11:185-194.
- LOWTHER, P. 1993. Brown-headed Cowbird (*Molothrus ater*). *In* A. Poole and F. Gill [EDS.], *The birds of North America*, No. 47. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- MARTIN, T. E., J. CLOBERT, AND D. R. ANDERSON. 1995. Return rates in studies of life history evolution: are biases large? *Journal of Applied Statistics* 22:863-875.
- MORRIS, M. J., AND R. E. LEMON. 1988. Mate choice in American Redstarts: by territory quality? *Canadian Journal of Zoology* 66:2255-2261.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler, *Dendroica discolor*. *Ornithological Monographs* 26.
- PART, T., AND L. GUSTAFSSON. 1989. Breeding dispersal in the Collared Flycatcher (*Ficedula albicollis*): possible causes and reproductive consequences. *Journal of Animal Ecology* 58:305-320.
- PAYNE, R. B., AND L. L. PAYNE. 1993. Breeding dispersal in Indigo Buntings: circumstance and consequences for breeding success and population structure. *Condor* 95:1-24.
- POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107.
- PORNELUZI, P. A. 1996. Effects of forest fragmentation on the biology of the Ovenbird. Ph.D. dissertation, University of Missouri, Columbia, MO.
- PORNELUZI, P. A., AND J. FAABORG. 1999. Season-long fecundity, survival, and viability of Ovenbirds in fragmented and unfragmented landscapes. *Conservation Biology* 13:1151-1162.
- VAN HORN, M., AND T. M. DONOVAN. 1994. Ovenbird (*Seiurus aurocapillus*). *In* A. Poole and F. Gill [EDS.], *The birds of North America*, No. 88. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- ZAR, J. H. 1984. *Biostatistical analysis*. Second edition. Prentice-Hall, Englewood Cliffs, NJ.