

## VARIABLE SONG RATES IN THREE SPECIES OF PASSERINES AND IMPLICATIONS FOR ESTIMATING BIRD POPULATIONS

W. J. MCSHEA AND J. H. RAPPOLE

*Conservation and Research Center, National Zoological Park  
Front Royal, Virginia 22630 USA*

**Abstract.**—Song rate in birds is known to be influenced by the social status and nutritional state of the male. However, studies examining the impact of management practices on the conservation of migratory species often use song rate techniques to census populations. We examined song rates in three species of forest birds in northwestern Virginia, and found that Wood Thrushes and Ovenbirds sang more often in blocks of continuous forest, while Northern Cardinals sang more often in forest patches. Individuals >50 m from the observer sang more often than closer birds, and individuals in higher density populations sang more often than individuals at low density sites. The spatial variability in song rate was not severe enough to significantly change species-detection rates for 5-min song counts, but did significantly affect our population density estimates for those species. A key assumption of song count censuses, that all individuals of a species sing at comparable rates and thus have an equal probability of being detected, regardless of habitat structure, may not be valid.

### TASAS VARIABLES DE CANTO EN TRES ESPECIES DE AVES PASERINAS Y SUS IMPLICACIONES AL ESTIMAR POBLACIONES DE AVES

**Sinopsis.**—Se sabe que la tasa de canto en aves es influenciada por el estatus social y la condición nutricional del macho. Sin embargo, estudios que examinan el impacto de prácticas de manejo en la conservación de especies migratorias a menudo utilizan técnicas basadas en tasas de canto para censar poblaciones. Examinamos las tasas de canto de tres especies de aves de bosque en el noroeste de Virginia y encontramos que individuos de *Hyllocichla mustelina* y de *Seiurus aurocapillus* cantaron más de corrido en porciones de bosques contiguos, mientras que individuos de *Cardinalis cardinalis* cantaron más comúnmente en parchos de bosque. Individuos a más de 50 m del observador cantaron más comúnmente que aves más cercanas, e individuos en poblaciones más densas cantaron más comúnmente que individuos en lugares con bajas densidades. La variabilidad espacial en tasas de canto no fué lo suficientemente severa como para cambiar significativamente las tasas de detección de especies para conteos de canto de 5 minutos, pero significativamente afectó nuestros estimados de densidad poblacional para estas especies. Una asunción clave de los censos basados en cantos, que todos los individuos de una especie cantan a tasas comparables y que por lo tanto tienen igual probabilidad de ser detectados independientemente de la estructura del hábitat, puede no ser válida.

Several hypotheses have been presented to explain vocal signalling by male birds (Catchpole 1982, Morton 1982, Searcy and Andersson 1986, Smith 1969). Most of these hypotheses assume that song has the adaptive function of signalling an individual's fitness, either to a competing male or to a potential mate. If this assumption is correct, then signal parameters, e.g., song type and rate, should vary according to the individual's status. Male song rate in several species has been correlated with the nesting stage of the pair (Wood Warbler, *Phylloscopus sibilatrix*, Termin 1986; Barn Swallow, *Hirundo rustica*, Møller 1991). Additionally, pair bond status has been found to affect song rate; unpaired males seeking mates sing more often than paired males (White-winged Dove, *Zenaida asiatica*, Rappole and Waggerman 1986; Kentucky Warbler, *Oporornis formosus*, Ovenbird, *Seiurus aurocapillus*, Gibbs and Wenny 1993). Physio-

logical state also can influence song rate. Food-supplemented males sang more than control males in the Pied Flycatcher (*Ficedula hypoleuca*) (Gottlander 1987), and song rate has been correlated with parasite load in Barn Swallows (Møller 1991).

Variability in individual song rates has significance for conservation biology. Song detection is the most frequently used method for assessing avian population size (see Hagan and Johnston 1992, Ralph et al. 1995, Ralph and Scott 1981, Robbins et al. 1989, Verner et al. 1986) despite indications that song frequency may not be a reliable indicator of population status (Baskett et al. 1978, Conner et al. 1983, Rappole and Wagerman 1986, Rappole et al. 1993). Based on song-count data, conclusions have been made regarding habitat preference (Freemark and Collins 1992), population change (Johnston and Hagan 1992), fragmentation effects (Blake and Karr 1987, Robbins et al. 1989), and forest management practices (Thompson et al. 1992). Avian productivity also has been measured indirectly by using the song rate of males to indicate breeding status (Gibbs and Faaborg 1990, Hagan et al. 1996, Van Horn et al. 1995).

A critical assumption for these methods is that song rate does not vary for individuals along temporal or spatial scales or by habitat (Caughley 1977, Mayfield 1981). Bart et al. (1995) examined the effects of extrapolating regional population trends based on counts made along roads, and found very little bias from this factor. However, it is well known that daily and seasonal variability can affect song rates (LaPerriere and O'Haugen 1972, Waechter 1977). Thus, standard count procedures specify temporal restrictions for song-based surveys, both in relation to sunrise and to peak breeding periods (International Bird Census Committee 1970, Skirvin 1981).

Variability of song rates along spatial scales or by habitat has been poorly documented. In one study, Gibbs and Faaborg (1990) found that Ovenbirds, but not Kentucky Warblers, were more often paired within continuous forest plots than within forest fragments, and, based on song surveys, concluded that differences in pair bond status could affect habitat-use comparisons.

The purpose of our study was to examine factors affecting song rate for three passerine species: two long distance migrants, the Wood Thrush (*Hylocichla mustelina*) and Ovenbird and one temperate resident, the Northern Cardinal (*Cardinalis cardinalis*). We tested the effects on individual song rates in males of these species of two spatial variables, forest patch size and distance to observer. Our goal is to determine the utility of song count data to estimate two measures commonly used in monitoring programs; presence/absence and population size.

#### METHODS

Song-rate counts for Wood Thrushes, Ovenbirds, and Northern Cardinals were conducted from 1–30 June in 1992 and 1993. Sites were located within isolated woodlots (forest fragments) of 4–24 ha and blocks of continuous forest >50 ha. All sites were located within a 30 km radius

of Front Royal, Virginia (78°08'W, 38°52'N), and contained a tree canopy composed of mature (>40 yrs) deciduous species. In 1992, 73 song-rate counts were conducted, with 34 counts at 32 forest fragments and 39 counts at 37 continuous forest sites. In 1993, 45 song-rate counts were conducted, with 22 counts at 17 fragment sites and 23 counts at 21 continuous sites. All counts were conducted >50 m from a forest edge and, when second counts were obtained from the same site, the second point was >250 m from the first point. The procedure for song-rate counts was to stop for 20 min at each site, identify individuals of targeted species by location, and count the total number of songs per individual over the 20-min period.

Point counts were also conducted at each site. The procedure for the point count followed standard protocols (Ralph et al. 1995), and was based on identifying all birds heard and/or seen during a 5-min period at each site. Point counts and song-rate counts were done sequentially at each site, with the point count completed first. For both point counts and song-rate counts, the location of each bird was noted as <50 m or >50 m from the observer. All point counts and song-rate counts were conducted between 0530–1000 h, under conditions of no rain and minimal wind velocity (i.e., <20 km/h). They were not conducted at sites on which mist-netting was underway in order to minimize effects of human disturbance. The same person (Grace G. Burford) conducted all of the point and song-rate counts to minimize variability due to observer.

To relate song rates to population density, the number of songs heard was compared to the number of individuals singing and the number of individuals captured by mist-netting at select sites. Each year at eight isolated forest sites and eight continuous forest sites, we conducted mist-netting during June, the peak of the breeding season in this area. The three focal species are all understory birds, and should be well-sampled using mist nets. We netted each site for 1000 net-hours, by placing 25 nets (12-m length, 2.6-m height, and 36-mm mesh) over a 4-ha area, and opening the nets at dawn each day for a 3–5-d period. All birds captured were identified, sexed, and given a unique numbered band. Using the mist-netting data, we compared the number of adult males captured with the number of birds heard during the point count for each species.

The song-rate count, i.e., the number of songs sung by an individual during a 20-min period, was compared for the variable classes of species, habitat, and distance to observer using parametric tests (multiple analysis of variance), except where assumptions of a normal distribution could not be met, in which case we used an extension of the Kruskal-Wallis test (Sokal and Rohlf, 1995:445; SAS Institute, Inc. 1987:715). There was no difference between years for song-rate counts (ANOVA, partial  $F = 2.11$ ,  $P = 0.146$ ) so data were pooled. Date and time of day were normally distributed, and proved to be marginally significant predictors of song rate ( $0.1 > P > 0.05$ ;  $r^2 = 0.01$ ; ANOVA), so the residuals from a regression equation using these variables were used for the Kruskal-Wallis test between class variables. A significance level of  $P < 0.05$  was used through-

TABLE 1. The mean ( $\pm$ SD) number of songs sung by an individual bird during 20 minutes for species, distance to observer, and forest habitat (Continuous and Fragment) at sites in northwestern Virginia during June 1992 and 1993. The sample size for each mean is given in parentheses. All class variables were significant predictors of song rate (Kruskal-Wallis test; see text), and for distance and forest habitat each species was then tested separately, with significant differences indicated.

Variable	Category	Species		
		Wood Thrush	Northern Cardinal	Ovenbird
Species**		67.0 $\pm$ 75.4 (292)	17.3 $\pm$ 21.1 (154)	18.0 $\pm$ 14.7 (52)
Distance > 50 m**	Yes	80.9 $\pm$ 82.3** (130)	20.1 $\pm$ 23.6 (74)	23.1 $\pm$ 14.4** (37)
	No	55.7 $\pm$ 67.5** (162)	14.7 $\pm$ 18.4 (80)	5.5 $\pm$ 3.6** (15)
Forest habitat*	Fragment	55.2 $\pm$ 58.3 (110)	18.7 $\pm$ 22.1** (126)	14.4 $\pm$ 16.1 (5)
	Continuous	74.1 $\pm$ 83.4 (182)	11.0 $\pm$ 15.2** (28)	18.4 $\pm$ 14.6 (47)

\*  $P < 0.05$ ; \*\*  $P < 0.01$ .

out. Chi-square was used to test for agreement between presence/absence counts using point count and mist-net capture data. Although we present only one measure of song rate, all significant differences reported using the number of songs heard/20 min were also significant when we used the number of minutes each bird sang/20 min.

## RESULTS

Song rates were determined for 498 birds over a 2-yr period. The species singing (Kruskal-Wallis;  $X^2 = 73.1$ ,  $P < 0.001$ ), the distance from the bird to the observer (Kruskal-Wallis;  $X^2 = 8.33$ ,  $P < 0.01$ ), and the habitat surveyed (Kruskal-Wallis;  $X^2 = 5.00$ ,  $P < 0.05$ ), significantly influenced the number of songs per bird heard over a 20-min period (Table 1). The variables measured can predict song rate, although they accounted for < 20% of the variability heard at the sites (ANOVA;  $F_{4,493} = 25.68$ ,  $r^2 = 0.17$ ,  $P < 0.001$ ). After accounting for the variability due to species differences (partial  $F = 43.3$ ,  $P < 0.001$ ), distance to observer and habitat type were still significant predictors of song rate (partial  $F = 11.76$ ,  $P = 0.001$  and partial  $F = 4.24$ ,  $P = 0.057$ , respectively). Most of the difference in song rate observed between habitat types was due to a single species, Northern Cardinal. However, there was a significant interaction between species and habitat type (partial  $F = 2.90$ ,  $P = 0.030$ ) indicating there are species-specific habitat effects on song rate.

Mean song rates for a species ranged from 67 songs/20 min (Wood Thrush) to 17 songs/20 min (Northern Cardinal). For Wood Thrushes and Ovenbirds, song rates were higher at continuous forest plots, while song rates were higher at forest fragments for Northern Cardinals (Table

TABLE 2. The mean ( $\pm$ SD) number of males detected during a 5 minute song census or 1000 net hours, for each species and each type of habitat. The surveys were taken during June 1992 and 1993 within northwestern Virginia forest habitats. We have only included sites with at least one individual of the species detected by either survey technique.

Technique	Species				Habitat	
	Wood Thrush ( $n = 17$ )	N. Cardinal ( $n = 10$ )	Ovenbird ( $n = 12$ )	All birds ( $n = 39$ )	Fragment ( $n = 11$ )	Continuous ( $n = 28$ )
Song count	1.44 $\pm$ 2.1	1.7 $\pm$ 1.3	0.58 $\pm$ 0.6	1.2 $\pm$ 1.2	1.9 $\pm$ 1.4	1.03 $\pm$ 1.1
Mist net	4.53 $\pm$ 3.8	2.3 $\pm$ 2.1	3.5 $\pm$ 1.3	3.8 $\pm$ 3.0	2.7 $\pm$ 1.9	4.18 $\pm$ 3.2

1). Each species sang more often in the habitat in which it was most abundant, as the number of birds heard at a site can be used to predict song rate (ANOVA,  $F_{1,496} = 13.52$   $r^2 = 0.13$ ,  $P < 0.003$ ).

The presence of the observer significantly depressed the song rate of the three species. Birds  $>50$  m from the observer sang twice as often as closer birds (Table 1).

The song survey and mist-netting techniques agreed significantly on the presence/absence of a species ( $X^2 = 20.5$ ,  $n = 75$ ,  $P < 0.001$ ). For sites where the species was detected during the 20-min census, the probability of detecting it during the first 3-min was higher in fragments than continuous forest ( $F_{5,181} = 6.44$ ,  $P < 0.001$ ), but the difference was due primarily to species composition (partial  $F = 14.6$ ,  $P < 0.001$ ) and not habitat type (partial  $F = 4.65$ ,  $P 0.03$ ). Habitat type did not explain a significant portion of the variation when the census period was extended to the first 5-min (partial  $F_{5,181} = 1.79$ ,  $P = 0.18$ ).

For sites where at least one individual was detected, there was a significant correlation between density estimates using the two techniques (Pearson product moment coefficient  $r = 0.44$ ,  $n = 39$ ,  $P < 0.001$ ). However, in only three cases were at least as many males detected by song as were captured in the mist-nets; an average of three times as many males were captured at a site as were detected during the song survey (Table 2). Whereas estimates based on the two survey techniques were relatively similar within forest fragment sites, an average of four times more males were captured than heard at continuous forest sites.

#### DISCUSSION

If individual song rates are sufficiently affected by experimental design (e.g., observer presence), social status of the individual male, or habitat features, then population parameters will be difficult to assess using any technique dependent on song detection. For the three species studied, individual song rates were variable at both the micro- and macrohabitat scale.

*Microhabitat.*—For the three species included in our study, the presence of an observer appeared to depress the song rate of birds within 50 m. This trend was more apparent for Ovenbirds, a ground-nesting species,

and less apparent for the other two species which tend to sing higher in the canopy. Detection of songs by observers also is influenced by habitat features that distort and attenuate the song (Richards 1981). Detection of the observer by the bird may be determined by sight distance, which would fluctuate with changes in weather conditions or habitat features, such as understory density. Thus, the occurrence of increased song detection for some forest species during foggy mornings (Robbins 1981) may be due in part to decreased sight distances. If visual detection of observers causes some species to reduce their song rates, density estimates based on song surveys at a fixed-radius point (e.g., Hutto 1992) may not be valid for comparisons between habitats that differ in sight distance.

*Macrohabitat.*—At a macrohabitat scale, individuals of forest interior species (Wood Thrush and Ovenbird) sang at higher rates within continuous forest than in fragmented forest, while the reverse was true for a thicket species, the Northern Cardinal. For each species, sites with the higher density of birds, as measured by mist nets, produced the higher song rates.

Song serves to attract mates and to advertise territorial boundaries to other males (Searcy and Andersson 1986). Gibbs (Gibbs and Faaborg 1990, Gibbs and Wenny 1993) argued that lack of pair bonding within suboptimal habitats resulted in increased song rates for unpaired males. Our data indicate that increased density, particularly of silent males, may also stimulate song rates.

Continuous forest sites contained more male Wood Thrushes that were not detected by song survey than did forest fragment sites. Regardless of whether these silent males are residents or transients, their presence may increase the song rate of territorial males. Increased song rate in response to unfamiliar birds has been documented in several species (Ydenberg et al. 1988 for review; European Robin *Erithacus rubecula*, Brindley 1991). For forest fragments, the isolation of the site may reduce the occurrence of transient birds, and thereby the song rate of residents. The lower number of forest interior birds detected within forest patches (Robbins et al. 1989) may be confounded by the lack of transient birds within these patches. Previous studies have found that observer sampling error increased with population density (Bart and Schoultz 1984, Desante 1981). Our results indicate that a bird's behavioral response to changes in population density could further confound ability to detect shifts in population numbers.

Shifts in song rate between habitats may also reflect changes in the nutritional state of males. Work on Pied Flycatchers (*Ficedula hypoleuca*) (Gottlander 1987) and Willow Warblers (*Phylloscopus trochilus*) (Radesater et al. 1987) indicates that song rate is a function of energy status. Lower song rates for forest interior birds within forest fragments may reflect reduced prey base for these species.

*Use of song counts for census data.*—Micro- and macrohabitat changes in song rate have not been considered in designing song survey protocols. The influence of habitat type on song rate do not appear to be severe

enough to prevent detection of a species, especially for census periods over 3-min. However, these spatial factors do result in significant differences in density estimates. Using song surveys to determine density, with comparisons between sites, or between years at the same site, must consider at least some of any observed change to be due to factors independent of population numbers. As suggested by Gibbs and Faaborg (1990) and Rappole et al. (1993), a single survey technique is not likely to be sufficient to detect changes in population numbers if social-based song rates are influenced by habitat. Surveys that combine song counts and mist-netting (e.g., Bollinger and Gavin 1992, Holmes et al. 1986) may offer the best solution. Accounting for temporal variability in individual song rate may be possible by restricting the survey period (although see Rappole et al. 1993); accounting for spatial variability in song rate may not be as tractable.

#### ACKNOWLEDGMENTS

Grace Burford made this project work with her effort and birding skills. We thank everyone who allowed us to survey birds on their land, particularly C. Burwell, P. Stokes, L. Walker, B. VonGontard, and Blandy Arboretum of the University of Virginia. Many individuals assisted with mist-netting, especially R. Scholl and D. Condoulis. We thank G. Morton and S. Derrickson for fruitful discussions on survey techniques, and J. Vega Rivera for reading an earlier draft of this manuscript. This work was supported primarily by the U.S. Fish and Wildlife Service, with some funds from National Fish and Wildlife Foundation, National Park Service, U.S. Forest Service, Earthwatch, Smithsonian National Associates, and Friends of the National Zoo.

#### LITERATURE CITED

- BART, J., M. HOFSCHEIN, AND B. G. PETERJOHN. 1995. Reliability of the breeding bird survey: effects of restricting surveys to roads. *Auk* 112:758-761.
- , AND J. D. SCHOULTZ. 1984. Reliability of singing bird surveys: changes in observer efficiency with avian density. *Auk* 101:307-318.
- BASKETT, T. S., M. J. ARMBRUSTER, AND M. W. SAYRE. 1978. Biological perspectives for the Mourning Dove call-count survey. *Trans. N. Amer. wildl. Nat. Res. Conf.* 37:312-325.
- BLAKE, J. G., AND J. R. KARR. 1987. Breeding birds of isolated woodlots: area and habitat relationships. *Ecology* 68:1724-1734.
- BOLLINGER, E. K., AND T. A. GAVIN. 1992. Eastern bobolink populations: ecology and conservation in an agricultural landscape. Pp. 497-505, *in* J. M. Hagen, III and D. W. Johnston, eds. *Ecology and conservation of neotropical migrant landbirds*, Smithsonian Inst. Press, Washington, D.C.
- BRINDLEY, E. L. 1991. Response of European robins to playback of song: neighbor recognition and overlapping. *Anim. Behav.* 41:503-512.
- CATCHPOLE, C. K. 1982. The evolution of bird sounds in relation to mating and spacing behavior. Pp. 297-319, *in* D. E. Kroodsma and E. H. Miller, eds. *Acoustic Communication in Birds*. Vol. 1, Academic Press, New York.
- CAUGHLEY, G. 1977. *Analysis of vertebrate populations*. John Wiley and Sons, New York.
- CONNER, R. N., J. G. DICKSON, AND J. H. WILLIAMSON. 1983. A comparison of breeding bird census techniques with mist netting results. *Wilson Bull.* 95:276-280.
- DESANTE, D. F. 1981. A field test of the variable circular-plot censusing technique in a California coastal shrub breeding bird community. *Stud. Avian Biol.* 6:177-185.
- FREEMARK, K., AND B. COLLINS. 1992. Landscape ecology of birds breeding in temperate forest fragments. Pp. 443-454, *in* J. M. Hagan, III and D. W. Johnston, eds. *Ecology and conservation of neotropical migrant landbirds*, Smithsonian Inst. Press, Washington, D.C.

- GIBBS, J. P., AND J. FAABORG. 1990. Estimating the viability of ovenbird and Kentucky warbler populations in forest fragments. *Conserv. Biol.* 4:193-196.
- , AND D. G. WENNY. 1993. Song output as a population estimator: effect of male pairing status. *J. Field Ornith.* 64:316-322.
- GOTTLANDER, K. 1987. Variation in song rate of the male Pied Flycatcher *Ficedula hypoleuca*: causes and consequences. *Anim. Behav.* 35:1037-1043.
- HAGAN, J. M. III, AND D. W. JOHNSTON, eds. 1992. Ecology and conservation of neotropical migrant landbirds. Smithsonian Inst. Press, Washington, D.C.
- , W. M. VANDER HAEGEN, AND P. S. MCKINLEY. 1996. The early development of forest fragmentation effects on birds. *Conserv. Biol.* 10:188-202.
- HOLMES, R. T., T. W. SHERRY, AND F. W. STURGES. 1986. Bird community dynamics in a temperate deciduous forest: long term trends at Hubbard Brook. *Ecol. Monog.* 56:201-220.
- HUTTO, R. L. 1992. Habitat distributions of migratory landbird species in western Mexico. Pp. 221-239, in J. M. Hagan, III and D. W. Johnston, eds. Ecology and conservation of neotropical migrant landbirds, Smithsonian Inst. Press, Washington, D.C.
- INTERNATIONAL BIRD CENSUS COMMITTEE. 1970. An international standard for a mapping method in bird census work recommended by the International Bird Census Committee. *Audubon Field Notes* 24:722-726.
- JOHNSTON, D. W., AND J. M. HAGAN, III. 1992. An analysis of long-term breeding bird censuses from eastern deciduous forests. Pp. 75-84, in J. M. Hagan, III and D. W. Johnston, eds. Ecology and conservation of neotropical migrant landbirds, Smithsonian Inst. Press, Washington, D.C.
- LAPERRIERE, A. J., AND A. O. HAUGEN. 1972. Some factors influencing calling activity of wild Mourning Doves. *J. Wildl. Manage.* 36:1193-1199.
- MAYFIELD, H. F. 1981. Problems in estimating population size through counts of singing males. *Stud. Avian Biol.* 6:220-224.
- MØLLER, A. P. 1991. Parasite load reduces song output in a passerine bird. *Anim. Behav.* 41:723-730.
- MORTON, E. S. 1982. Grading, discreteness, redundancy and motivation structural rules. Pp. 183-212, in D. E. Kroodsma and E. H. Miller, eds. *Acoustic Communication in Birds*. Vol. 1, Academic Press, New York.
- RADESATER, T., S. JAKOBSSON, N. ANDBJER, A. BYLIN, AND K. NYSTROM. 1987. Song rate and pair formation in the Willow Warbler, *Phylloscopus trochilus*. *Anim. Behav.* 35:1645-1651.
- RALPH, C. J., AND J. M. SCOTT, eds. 1981. Estimating numbers of territorial birds. *Stud. Avian Biol.* 6:1-630.
- , S. DROEGE, AND J. R. SAUER. 1995. Managing and monitoring birds using point counts: Standards and Applications. Pp. 161-168, in C. J. Ralph, J. R. Sauer, and S. Droegge, eds. *Monitoring bird populations by point counts*. U.S.D.A. Forest Service general Report PSW-GTR-149.
- RAPPOLE, J. H., W. J. MCSHEA, AND J. VEGA RIVERA. 1993. Evaluation of two survey methods in upland avian breeding Communities. *J. Field Ornithol.* 64:55-70.
- , AND G. WAGGERMAN. 1986. Calling males as an index of density for breeding White-winged doves. *Wildl. Soc. Bull.* 14:151-155.
- RICHARDS, D. G. 1981. Environmental acoustics and censuses of singing birds. *Stud. Avian Biol.* 6:297-300.
- ROBBINS, C. S. 1981. Bird activity levels related to weather. *Stud. Avian Biol.* 6:301-310.
- , D. K. DAWSON, AND B. A. DOWELL. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic States. *Wildl. Monogr.* 103:1-34.
- SAS INSTITUTE, INC. 1987. SAS/STAT Guide. Version 6 Edition. SAS Institute Inc., Cary, North Carolina.
- SEARCY, W. A., AND M. ANDERSSON. 1986. Sexual selection and the evolution of song. *Ann. Rev. Ecol. Syst.* 17:307-333.
- SKIRVIN, A. A. 1981. Effect of time of day and time of season on the number of observations and density estimates of breeding birds. *Stud. Avian Biol.* 6:271-274.
- SMITH, W. J. 1969. Messages in vertebrate communication. *Science* 165:145-150.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*. W. H. Freeman and Company, New York.



- TERMIN, H. 1986. Singing behaviour in relation to polyterritorial polygyny in the wood warbler (*Phylloscopus sibilatrix*). *Anim. Behav.* 34:146–152.
- THOMPSON, F. R., W. D. DIJAK, T. G. KULOWIEC, AND D. A. HAMILTON. 1992. Breeding bird populations in Missouri Ozark forests with and without clearcutting. *J. Wildl. Manage.* 56:23–30.
- VAN HORN, M. A., R. M. GENTRY, AND J. FAABORG. 1995. Patterns of Ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. *Auk* 112:98–106.
- VERNER, J., M. MORRISON, AND C. J. RALPH, eds. 1986. *Wildlife 2000: Habitat relationships of terrestrial vertebrates*. Univ. Wisconsin Press, Madison, Wisconsin.
- WAECHTLER, D. G. 1977. Electronic call-counts as an indicator of nesting white-winged dove populations. M.Sc. thesis. Texas A&I Univ., Kingsville, Texas. 48 pp.
- YDENBERG, R. C., L. A. GIRALDEAU, AND J. B. FALLS. 1988. Neighbors, strangers and the asymmetric war of attrition. *Anim. Behav.* 36:343–347.

Received 14 Mar. 1996; accepted 5 Sep. 1996.