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SONG OUTPUT AS A POPULATION ESTIMATOR: EFFECT OF MALE PAIRING STATUS

JAMES P. GIBBS[1] AND DANIEL G. WENNY[2]
Division of Biological Sciences
105 Tucker Hall
University of Missouri–Columbia
Columbia, Missouri 65211 USA

Abstract.—Variation in song output of paired and unpaired, male Ovenbirds (*Seiurus aurocapillus*) and Kentucky Warblers (*Oporornis formosus*) was examined and its effect on estimates of population density derived from the spot-map survey technique. Song output during late-May and early-June in central Missouri averaged 3.5 times greater for 17 unpaired (1.74 songs/min) than 15 paired Ovenbirds (0.50 songs/min) and 5.4 times greater for 16 unpaired (2.22 songs/min) than 26 paired Kentucky Warblers (0.41 songs/min). Ten spot-map visits to known populations detected all unpaired males but missed 50% of paired male Ovenbirds and 35% of paired male Kentucky Warblers. A reliance on singing male contacts during spot-map surveys resulted in underestimation of population density and could confound assessments of habitat quality.

EL CANTO UTILIZADO PARA ESTIMAR EL TAMAÑO DE POBLACIONES: EL EFECTO DE MACHOS APAREADOS Y NO-APAREADOS

Sinopsis.—Se estudió la variabilidad en la producción de cantos por parte de machos pareados y no-pareados de pizpita (*Seiurus aurocapillus*) y reinita de Kentucky (*Oporornis formosus*), para determinar su efecto en estimados de densidad poblacional utilizando la técnica de puntos en mapas (*spot-map*). La producción de cantos (durante el final de mayo y principios de junio) en la parte central de Missouri, resultó ser (en promedio) 3.5 veces mayor en 17 pizpitas no-apareadas (1.74 cantos/min) que en 15 individuos pareados (0.50 cantos/min) y 5.4 veces mayor para 16 reinitas de Kentucky no-apareadas (2.22 cantos/min) que en 26 de estas pareadas (0.41 cantos/min). Diez censos, utilizando la técnica de puntos en mapas, permitieron localizar todos los machos no-apareados, pero tan sólo al 50% de las pizpitas pareadas y el 35% de las reinitas de Kentucky con parejas. El utilizar el canto de machos para hacer censos, de tipo puntos en mapas, da lugar a subestimados, y puede traer confusión cuando se trata de determinar la calidad de un habitat.

Many methods for surveying bird populations rely on counts of singing males, and between 80–90% of detections during count periods are typically aural (Best 1981, Scott et al. 1981). Most survey methods assume that each individual in a population has the same average probability of being detected (Caughley 1977); variation in singing activity among males may thus bias estimates of population density (Sayre et al. 1980, Wilson and Bart 1985). Singing activity varies in relation to time of day (Robbins 1981, Shields 1979, Skirvin 1981), temperature (Garson and Hunter 1979), and time of season (Best 1981, Skirvin 1981). Mating status also is known to affect dramatically song output (Best 1981, Cuthill and

[1] *Current address: School of Forestry and Environmental Studies, Yale University, 205 Prospect St., New Haven, Connecticut 06511 USA.*
[2] *Current address: Department of Zoology, 223 Bartram Hall, University of Florida, Gainesville, Florida 32611 USA.*

Hindmarsh 1985, Hayes et al. 1985, Johnson 1983), and unpaired males of monogamous species typically sing more frequently than paired males.

In this study we assessed whether population surveys that rely on counts of singing males could be biased toward unmated males. We measured variation in the singing activity and relative detectability of male Ovenbirds (*Seiurus aurocapillus*) and Kentucky Warblers (*Oporornis formosus*) in relation to male mating status, and conducted a field test to examine the effectiveness of the spot-map technique for detecting paired and unpaired males in known populations of these two species.

METHODS

Study areas.—We used eight sample plots, 20–35 ha in size, located in Boone and Callaway counties in central Missouri on lands of the Mark Twain National Forest's Cedar Creek Unit (38°54′N, 92°4′W), the University of Missouri's Ashland Wildlife Research Area (38°44′N, 92°12′W), and on private holdings near Fulton (38°53′N, 92°57′W). All sites were dominated by upland, mature oak (*Quercus* spp.)-hickory (*Carya* spp.) deciduous forest.

Mating status determinations.—Between 2 and 14 May 1988, study areas were surveyed daily between sunrise and 3 h after sunrise to locate territorial males. Mating status of territorial males was determined between 15 May (approx. 3–4 wk after the birds' arrival in central Missouri when most pairing activity had presumably already occurred) and 15 June (when fledglings of both species began to appear in substantial numbers and further breeding activity seemed unlikely). Individual focal males (Altmann 1974) were followed continuously for 90-min periods and carefully observed for any evidence of being paired, such as being observed within 5 m of a female, carrying nest material, or feeding young (including Brown-headed Cowbird, *Molothrus ater,* young). All paired males were classified well before the 90-min observation period had lapsed (Ovenbirds at ≤67 min, Kentucky Warblers at ≤52 min), so most pairing-status determinations likely were valid (cf. Probst and Hayes 1987). All observations were made between sunrise (about 0545 hours) and 1000 hours on days without precipitation. During observation periods, locations of nearby singing males were noted on maps of study sites. Between observation periods, suitable habitat between known territories was surveyed by playing pre-recorded cassette tapes (Kellogg et al. 1975) of songs of both species.

Measurement of male song output and detectability.—Song output of focal males was simultaneously recorded during mating status determinations. We restricted our observations of males to the egg-laying and incubation periods when differences between song output levels of paired and unpaired males typically are greatest (Best 1981, Wilson and Bart 1985). A continuous, 90-min record of each bird's singing activity was compiled by noting when a focal bird sang (to the nearest second). Observations were recorded by dictating song output times, read off of a running stopwatch, into a cassette tape recorder. Both species sing a simple song

of a single type, with each song consisting of from four to six repetitions of identical syllables (Tsipoura and Morton 1988). Song records were later re-examined to estimate the extent to which paired versus unpaired males were detectable by a hypothetical field observer listening for birds over intervals ranging from 1 to 10 min. Each song record was sampled three times at randomly determined, non-overlapping points. Whether a bird sang (detectability = 1) or was silent (detectability = 0) during each sample was noted. Detectability values equalled the proportion of total samples in which birds sang.

Effects of two environmental variables on song output, time of day and season, also were assessed. We calculated the average number of songs output/minute by focal males during each 15-min period of observation, and contrasted song output by different categories of time of day (hours after sunrise: 0–0.9, 1–1.9, 2–2.9, ≥3) and season (15–31 May vs. 1–15 Jun.) with a Kruskal-Wallis nonparametric analysis of variance (Zar 1984).

Field assessment of the spot-mapping technique.—Portions of our study areas with known populations of Ovenbirds and Kentucky Warblers were simultaneously and independently surveyed by four individuals employing the spot-map technique and following procedures outlined by Robbins (1970). Areas were surveyed between 0530 and 1000 hours on mornings between 15 May and 30 Jun. 1988. Ten visits per site were made. Maps of territory locations, as indicated by a minimum of three clustered spot-observations (both aural and visual contacts), were later compared to maps of territory locations derived from our intensive surveys of study plots.

RESULTS

Song output.—Song output of 17 unpaired Ovenbirds (mean = 1.74 ± 0.76 [SD] songs/min) was 3.5 times greater than that of 15 paired males (0.50 ± 0.35 songs/min; $t = 5.77$, $P < 0.001$). Song output also differed among Kentucky Warblers ($t = 8.04$, $P < 0.001$), with 16 unpaired males singing 5.4 times as frequently (2.22 ± 0.87 songs/min) as 26 paired males (0.41 ± 0.56 songs/min). Song output did not vary among the 4-h-long periods following sunrise for paired Ovenbirds (Kruskal-Wallis test: $\chi^2 = 4.72$, $P = 0.193$, df = 3, 74), unpaired Ovenbirds ($\chi^2 = 3.91$, $P = 0.271$, df = 3, 80), or paired Kentucky Warblers ($\chi^2 = 3.55$, $P = 0.315$, df = 3, 117). Song rates in unpaired Kentucky Warblers, however, were slightly higher ($\chi^2 = 6.49$, $P = 0.090$, df = 3, 64) 1–2 h after sunrise (2.5–2.7 songs/min) than 3–4 h after sunrise (1.7–1.8 songs/min). Season (late May vs. early June) had no effect on singing frequency in paired Ovenbirds (Kruskal-Wallis test: $\chi^2 = 1.89$, $P = 0.119$, df = 3, 76). Lateness of season, however, strongly reduced song output in unpaired Ovenbirds (1.97 vs. 1.37 songs/min, $\chi^2 = 8.75$, $P = 0.0041$, df = 1, 82) and unpaired Kentucky Warblers (3.77 vs. 1.98 songs/min, $\chi^2 = 16.10$, $P = 0.001$, df = 1, 59), and elevated song output in paired Kentucky Warblers (0.035 vs. 0.45 songs/min, $\chi^2 = 7.66$, $P = 0.0057$, df = 1, 120).

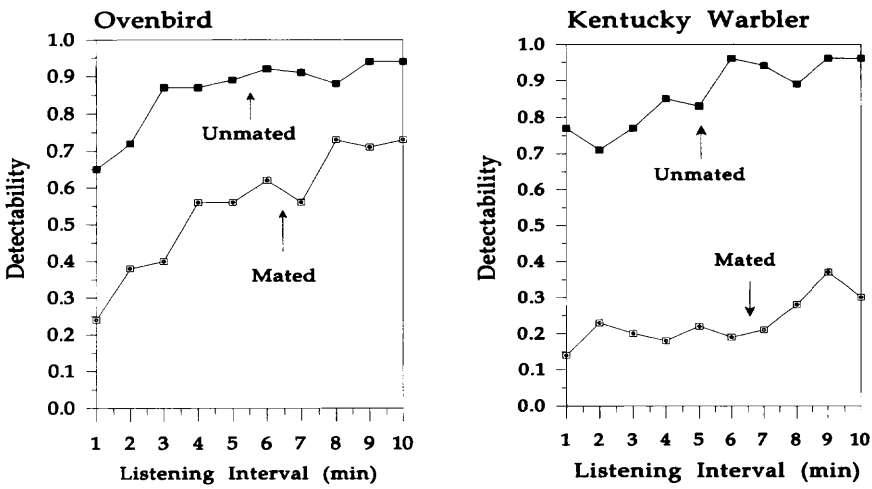

FIGURE 1. Probability that paired and unpaired male Ovenbirds and Kentucky Warblers sang at least once in relation to length of listening interval.

Detectability.—Substantial differences in detectability of paired versus unpaired males in both species were evident at listening intervals <5–6 min (Fig. 1). At listening intervals approaching 10 min, however, detectability of paired and unpaired male Ovenbirds nearly converged, whereas detectability of paired and unpaired Kentucky Warblers remained disparate (Fig. 1).

Population surveys.—Adequate spot-map estimates were made of numbers of unpaired male Ovenbirds and unpaired male Kentucky Warblers occupying study areas, but numbers of paired male Ovenbirds were underestimated by 50% and paired male Kentucky Warblers by 35% (Table 1). An examination of a random sample of 25 daily spot-maps indicated that field observers relied heavily on singing male contacts when making field registrations of Ovenbirds (95.6% of contacts) and Kentucky Warblers (79.4%). Visual and non-song, aural contacts comprised remaining registrations.

TABLE 1. Numbers and proportions of paired and unpaired male Ovenbirds and Kentucky Warblers detected by the spot-map technique on eight study plots in central Missouri in 1988.

Mating status	Present	Detected (%)
Ovenbird		
Unpaired	15	15 (100)
Paired	14	7 (50)
Kentucky Warbler		
Unpaired	7	7 (100)
Paired	23	15 (65)

DISCUSSION

Implications for population estimation.—Variation in song output of male songbirds represents an important source of error in field methods that rely on singing male contacts to estimate populations. Observers in our study relied heavily on song to locate birds and hence detected unpaired male Kentucky Warblers and Ovenbirds more readily than paired males. Consequently, unpaired males were adequately represented on final territory maps whereas paired males often were overlooked. Similarly, Best and Peterson (1982) observed that spot-map surveys were biased toward unmated males, that paired males often went undetected, and that overall population density was underestimated.

Paired males were underrepresented on our final spot-map tallies to a greater extent than might be predicted based on singing frequency alone. For example, detection probabilities of paired male Ovenbirds over a 3-min listening period (i.e., 0.40) suggest that the likelihood of recording birds on three or more out of 10 visits was 83% (Zar 1984:371–372), but 50% of paired male Ovenbirds were overlooked during our spot-map surveys. In addition to reduced overall singing activity, brevity of singing bouts in paired male Ovenbirds, which typically were limited to just 1–2 songs, may have reduced their detectability. Although recorded readily by an observer closely monitoring song output of a focal male, such brief song bouts may often have failed to attract the attention of field observers walking through the study area conducting spot-map surveys. Other behavioral traits of paired males may have further contributed to their reduced detection rates. For example, unlike unpaired male Overbirds that usually sang from elevated song perches, paired males typically foraged and sang inconspicuously at ground-level among herb and shrub cover where they were difficult to locate aurally and visually.

Extended listening periods (5–10 min) during spot-map visits could improve detectability of paired male Ovenbirds. Our data indicate, however, that the infrequent song output of paired male Kentucky Warblers made detecting them on the basis of song alone difficult (detectability <0.5), even after a 10 min listening interval. Increasing the number of survey visits thus appears to be a more productive means of improving the detectability of Kentucky Warblers than increasing the listening time of each visit.

As observations of singing males likely comprise the majority of observations in many survey efforts (van Riper 1981), further comparisons between the detectability of paired and unpaired males are needed in other species of songbirds to assess the pervasiveness of the bias in detectability associated with mating status. Furthermore, the relative importance of the bias on single-visit surveys, such as transect counts, versus on multiple visit surveys, such as spot-mapping censuses, should be assessed.

Implications for habitat assessment.—Distributions of paired and unpaired males are not constant among habitats. Spot-mapping in high

quality habitats, occupied primarily by infrequently singing, mated males (Ficken and Ficken 1966, 1967; Gibbs and Faaborg 1989; Morse 1973; Probst and Hayes 1987), may reveal few territorial individuals, whereas surveys in lower quality areas, frequented by unpaired, more vocal males, may detect relatively more individuals. Hence, among species in which pairing status exerts a strong influence on singing behavior, a reliance on song output as a population estimator may potentially confound field assessments of bird habitat quality. Variation in average singing rates among populations occupying different habitats could provide an index of habitat quality, however, if differences in song output between paired and unpaired males of a species are quantified and song output of all individuals comprising different populations is sampled with equal intensity.

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Harold E. Burtt (1890–1991)

It is the sad fate of a few ornithologists to outlive all their associates and pass from this life almost without notice from the ornithological world. Such was the case of Harold E. Burtt, who died 15 Aug. 1991, at Columbus, Ohio, at the age of 101. His interest in birds was incidental to his main vocation, but it was considerable. At his backyard station he banded 164,054 birds, and his book, "Psychology of Birds," 1967, Macmillan, New York, was unusual, if not unique, in having been written by a distinguished professional in human psychology. Burtt was not known widely in ornithology, but he was world-famous in his field and one of the founders of industrial psychology. He headed the Psychology Department at Ohio State University for more than 20 yr. Ornithology should be proud to lay some claim to him.