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PROBLEMS IN ESTIMATING POPULATION SIZE THROUGH COUNTS OF SINGING MALES

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ABSTRACT.—Counts of singing males in breeding season appear to be an easy way of estimating bird populations, but detailed studies of such typical songbirds as Kirtland's Warbler and Prairie Warbler show enormous variability in song frequency for different species, different individuuals, different stages of reproduction, different hours of the day, and different weather conditions; and these uncertainties are compounded by the fact that sex ratios are seldom known accurately. Consequently, censuses often contain errors much larger than customarily encountered in scientific measurements. Under ideal conditions the probability of hearing a male Kirtland's Warbler within a 5-minute period is about .85, and the probability of hearing a male Prairie Warbler is about .55. To test my census efficiency on an assortment of familiar species, I conducted transect counts on ten consecutive days in early June at the 2½ hectare tract surrounding my own home. This test showed census efficiencies for different species ranging from zero to 90%, and the average efficiency for all species of 40–50%. Counts of males are commonly translated into population totals by assuming one female for each male. Yet the difficulty of determining exact sex ratios is illustrated by the Brown-headed Cowbird, for which published estimates vary by 30% or more, and my own 5-year sample of 18,000 birds taken on the breeding grounds showed a high predominance of females early in the season and a high predominance of males at later dates, suggesting large differences in mobility but leaving the true ratio in question. From my experience I have concluded (1) some species cannot be counted effectively by brief listening periods, (2) difficulties with each species can be appraised only through lengthy study of each, and (3) people studying the behavior and reproduction of birds should direct attention to problems of censusing to be expected by others.

J. T. Emlen (1971, 1977a) has written comprehensively on methods of censusing bird populations and their shortcomings. Of all the methods available, one of the most attractive for use with small land birds is the count of singing males. It looks easy because pairs during the nesting season are anchored to exclusive territories, and the males advertise their presence loudly. I have used it for many years with the Kirtland's Warbler (*Dendroica kirtlandii*), and through experience have become increasingly conscious of sources of error with the best of subjects and appalled by the potential error with more difficult subjects. The errors are much larger than customarily expected in scientific measurements, and usually they are not quantified or even acknowledged.

Here I will focus attention on two sources of uncertainty that I have examined: (1) the probability that a male will not be detected on its territory in a brief census period, and (2) the ratio of males to females needed to calculate the total population size. This information is not available for most species with precision. My examples are drawn, first, from closely-related warblers familiar to me and studied in depth, particularly the Kirtland's Warbler studied by me for 18 years and the Prairie Warbler (*Dendroica discolor*) studied for 21 years by Val Nolan; second, from ten consecutive daily censuses on my own property where the resident birds were already known; and third, from very large samples of Brown-headed Cowbirds (*Molothrus ater*) collected over five breeding seasons in a unique effort at total removal of this parasite from the nesting grounds of the Kirtland's Warbler.

VARIATIONS IN WARBLER SONG

In my first census of the entire population of Kirtland's Warblers in 1951 (Mayfield 1953:18–20), I reported 432 singing males, and since that time I have cringed at calculations based on this exact number. At the time I expressed the reservation that the count might have been understated by as much as 25% for various reasons, and in later accounts I usually rounded the count to 500. Nevertheless, the exact figure persists, and the reservations are usually forgotten.

With thought to census needs, I attempted to assess the probability a Kirtland's Warbler would be heard by a person walking slowly through its territory during nesting season (Mayfield 1960:130–135). Under ideal conditions the song can be heard at a distance of 400 m, the full width of a male's territory. Like most songbirds, it gives its song in courses. Songs lasting 1–1½ seconds are uttered 6–9 times a minute, but these courses of song may be interspersed with periods of silence lasting many minutes. When I analyzed detailed records of song gathered at various nesting stages, dividing the periods of time into segments of 5 minutes each, I found that 85% of 480 time segments contained at least one song, and thus the probability a male would be heard in one passage through his territory was about .85. The Kirtland's Warbler proves to be an almost ideal subject for censusing, and through repeated counts on familiar

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areas in succeeding years, we believe our accuracy has improved. Still we cannot place complete confidence in these stated probabilities because of possible selectivity in our song samples. Poor singers are less likely to get into the records.

Kirtland's Warbler males behaving in standard fashion can be counted fairly accuragely by visiting each "colony" a few times or walking back and forth through it several times at the height of the nesting season, provided the weather is good and the hour of the day is early. This belief has been confirmed by intensive field work on censused areas. But even under ideal conditions, we may wonder how many males are *not* behaving in standard fashion. Although the species sings persistently through all stages of the nesting process, males are sometimes unaccountably silent for hours at a time. More than once I have searched in vain for an hour where a male was believed to be present, and then later have found it readily. I have concluded that males leave their territories more often than generally realized. For example, I once found a banded male (believed unmated) singing as though on territory 2 km from his home site. Only by accident was he discovered. How many such did I miss? Also during my work in a small isolated "colony" where all the resident males were banded and recognized by idiosyncracies of song, I occasionally detected unknown males slipping through the area silently. Previous authors have named such males "floaters," implying that they are nonbreeding males without territories drifting through occupied regions, perhaps ready to fill any vacancies that occur. However, Norman Ford (unpubl. data) has expressed doubt that such floaters exist among the Yellow Warblers (*Dendroica petechia*) he has studied on one tract of land for several years. Instead, he believes these are mated, territorial males reconnoitering away from home. Nolan (1978:362) reached similar conclusions about Prairie Warblers. Whatever the mechanisms, it is clear there is flexibility in movements and bonds, allowing lost mates to be replaced quickly in many cases. We also have instances where males have occupied two territories simultaneously, with or without polygyny. Ordinarily it is assumed such anomalies are so rare they can be ignored in calculations. Yet Nolan's (1978:364–365) study of the Prairie Warbler is not reassuring on this point. He found polygyny occurring in about 15% of male Prairie Warblers, and sometimes it involved separate or elongated territories that could have been disentangled only by prolonged study.

In his transect counts J. T. Emlen (1971) employed a "coefficient of detectability" to deal with differences in the distances at which species reveal themselves, as it affects the strip-width being censused in a transect. The distances species may be heard vary enormously, and so do the singing habits of species and individuals within a species. The uncertainties caused by periods of silence, immobility, and absence are very large in some species. In addition to the characteristic elusiveness of some birds, we need to consider variations for different stages of the nesting season, for different hours of the day, for different weather conditions, and for individual differences within each species. Consequently, to proceed from a count or a series of them to an accurate determination of population size may require knowledge based on a prodigious amount of field work.

The Prairie Warbler is a persistent singer, but Nolan (1978:64, 71) found some of them silent more than twice as much of the time as others on the same date, and at different reproductive stages he found song frequencies for the same individual varying in the ratio of four to one. He has supplied me with details on seven extended periods of song by males with active nests in various stages. He divided the time into 5-minute segments, noting whether or not song took place in each of these. Considering only the first five hours of daylight (before 10:00), I have analyzed a sample of 405 segments. Of these, 224 (55%) contained at least one song. Hence, the probability of detecting one of these birds in a 5-minute listening period was about .55. The variability among individual birds, however, was startling. One bird sang for 15 minutes very early in one morning and then was silent for three hours, while another was almost silent during the first two hours and then sang frequently later in the morning. One bird sang in 90% of one morning's 5-minute segments; yet another male sang in only 25% of them.

In his study of Yellow Warblers, Ford (unpubl. data) found males to be relatively quiet during days of nest building. On the other hand, males of this species and many others are most vocal when unmated, but their conspicuousness at one location may be offset by a greater tendency to stray and sing elsewhere.

CENSUSING AN ASSEMBLAGE OF SPECIES

Up to this point I have considered census problems with species whose behavior has been studied thoroughly. Usually the person conducting a census is faced with the more difficult problem of dealing with a variety of birds whose habits are not known to him in detail. One way to appraise the accuracy of such a count is to conduct it on a tract that is already under such

TABLE 1
COUNTS OF SINGING MALES ON TRACT NEAR WATERVILLE, OHIO, 1980

Song freq.[a]	Species	Date in June										Total times counted	Pairs actually present	Maximum possible count	% eff.
		6	7	8	9	10	11	12	13	14	15				
.40	Mourning Dove		1		1		1	2	1	2	2	10	3	30	33
	Yellow-billed Cuckoo									1		1	1	10	10
	Ruby-thr. Hummingbird											0	1	10	0
	Downy Woodpecker			1	1			1				3	1	10	30
	E. Wood Pewee	1			1	1	1	1	1	1	1	8	1	10	80
	Blue Jay		1									1	1	10	10
	Tufted Titmouse								1		1	2	1	10	20
	White-br. Nuthatch				1				1			2	1	10	20
.66	House Wren	4	3	4	3	4	3	4	4	4	3	36	4	40	90
.44	Catbird		1		1	1	1	1	1	1	1	8	1	10	80
.19	Robin	1	1	3	1	2	3	3	2	2	2	20	4	40	50
	Cedar Waxwing									1	1	2	1	10	20
	Starling					1			1		1	3	1	10	30
.10	Northern Oriole	1	1		1	1			1		1	6	1	10	60
	Common Grackle		1	1	2	1	1	1	1	2	2	12	4	40	30
.51	Brown-h. Cowbird								1			1	1	10	10
.59	No. Cardinal	1	1	1			2		1	3	1	10	3	30	33
.53	Indigo Bunting	1	1	1			1	1		1	1	7	1	10	70
	Chipping Sparrow									1		1	1	10	10
.75	Song Sparrow		1							1	1	3	1	10	30
Hours after sunrise		3	2	2	2	1	2	1	2	1	1				

[a] Song frequency from Emlen (1977b:461) approximately equivalent to percent efficiency here.

close scrutiny, preferably by different observers, that the residents are thoroughly known (see DeSante 1981, Hildén 1981). Excellent opportunities for such tests are presented at research stations where several people are already engaged in separate projects.

To explore this problem in a preliminary way, I conducted ten censuses of the birds at my own home. I was familiar with the birds present, having observed them before and after they set up territories. On 10 consecutive mornings between one and three hours after sunrise, June 6–15, 1980, I walked slowly down the middle of my property for its entire length. The strip was 250 m in length, and I took 10–14 minutes for the route. Thus, my walking speed was about 1 km per hour, roughly comparable to Emlen's transect walking speed and Robbins' (1979b) 3-minute listening stops, since I progressed less than 100 m in each 3 minutes. I believe no song escaped me within 50 m on either side of my path and some birds were heard at greater distances, and I thus considered the area covered to be roughly 2½ hectares.

This tract was mostly covered with mature trees, under which lay mowed lawn, many shrubs, and, at the end near a river, undisturbed underbrush. It had sharp ecological boundaries at each each end—a highway and cultivated field at one end and a 100 m wide river at the other. The sides, however, had no natural boundaries. One of the long sides overlapped a brushy abandoned orchard, and the other adjoined lawns and woodland like my own. An ecological island would have been better. At this time of year the vegetation was in full leaf, and visibility was severely limited in the canopy and in the brushy understory.

Since my ultimate interest was to determine the total population, I noted all birds seen as well as heard, and recorded the numbers in terms of pairs rather than individuals (Table 1); that is, a family out of the nest, a pair seen together, or a singing male were each recorded as one pair. I judged 33 pairs of 20 species to be resident, but I had some troublesome decisions in arriving at these arbitary numbers. Although not every nest was found, and some known nests were being lost and replaced at new locations, all of these residents were believed to be nesting on or immediately adjacent to the census area, with territories overlapping it. However, even in this familiar situation, I was troubled with uncertainties about which birds were properly to be considered residents or merely visitors. I excluded from the set of birds "actually present" several species known to be in the vicinity but not believed to be occupying it regularly at the date of the censuses. One such was the Wood Thrush (*Hylocichla mustelina*),

which nested on the tract regularly in previous years, and sang here before and after the test period but was not detected at any time during the 10-day interval. Others also excluded after internal debate were water and shorebirds, swallows and swifts, Common Flicker (*Colaptes auratus*), Hairy Woodpecker (*Dendrocopus villosus*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), and American Goldfinch (*Spinus tristis*). Still other species were seen here from time to time, and including them or not seriously affects the calculated census efficiency.

My census efficiency ranged from zero to 90% for different species. Lumping all the species I admitted into my sample, my efficiency for the entire set was 40%. When I omitted certain species judged unsuitable or doubtfully suitable for a census of this kind, my efficiency approached 50%; that is, I detected about half the pairs actually present and reasonably expected to be found in such a count. The birds of my set presenting difficulties because of wide-ranging habits or inconsistent song were as follows: Yellow-billed Cuckoo (*Coccyzus americanus*), Ruby-throated Hummingbird (*Archilochus colubris*), Downy Woodpecker (*Dendrocopus pubescens*), Blue Jay (*Cyanocitta cristata*), Tufted Titmouse (*Parus bicolor*), White-breasted Nuthatch (*Sitta carolinensis*), Cedar Waxwing (*Bombycilla cedrorum*), Starling (*Sturnus vulgaris*), and Brown-headed Cowbird. The most reliable subjects, with every male detected on more than 70% of the counts, were House Wren (*Troglodytes aedon*), Catbird (*Dumetella carolinensis*), Eastern Wood Pewee (*Contopus virens*), and Indigo Bunting (*Passerina cyanea*). Others more likely to be seen than missed in a quick count, with every male found on more than half the censuses, were Northern Oriole (*Icterus galbula*) and Robin (*Turdus migratorius*). However, since the numbers of birds in this sample are very small, these figures may reflect individual as much as species characteristics.

Surprises lay at the other end of the scale. It seemed remarkable that such a conspicuous and noisy species as the Blue Jay, which was seen many times each day, appeared only once in the test counts. It was also surprising to hear the song or call of the Chipping Sparrow (*Spizella passerina*) only once, although it was feeding fledglings on the area, and I could find it by deliberate search every time. In many species it was apparent a count earlier in the season would have yielded different results. Starlings and Common Grackles (*Quiscalus quiscula*) were already feeding large flying young and were ranging far beyond the census strip. Some Mourning Doves (*Zenaida macroura*) were between nestings, and Cedar Waxwings had not yet begun. Any date chosen will be wrong for some pairs.

No bird sings continuously, and a bird in heavy foliage is not likely to be detected if silent during a brief period of observation. For example, the Northern Oriole and Catbird, which were among the most reliable subjects in this test, were never seen on any of the counts. Had they been less vocal, like the Yellow-billed Cuckoo or Ruby-throated Hummingbird, they would not have been detected at all. These last two species I judged unsuitable for this kind of census at any season. Even birds we regard as conspicuous, like the Northern Cardinal (*Cardinalis cardinalis*) and Tufted Titmouse, were seldom detected when not singing. The female Brown-headed Cowbird was seen only once and the male not at all, although she laid several eggs on the tract during this period.

My results showed very loose correspondence for some of the species of Emlen's (1977b:461–462) study of a 48 acre tract of woodlands in Wisconsin, which also identified the House Wren, Catbird, Cardinal, and Indigo Bunting among the more dependable singers, but some differences in our findings were notable. For example, he heard the Northern Oriole much less often than I did; I detected the Brown-headed Cowbird rarely (female only), and he found it half the time; my pair of Song Sparrows (*Melospiza melodia*), which had nests on this tract before and after the study period, revealed themselves to me in only one-third of my counts, while his Song Sparrows sang on three-fourths of his transects. This enormous variability reminds us to expect large errors in brief surveys and small samples.

DIFFICULTIES WITH SEX RATIOS

Thus far I have been concerned with uncertainties in the counts themselves and have not mentioned a further step required to go from the number of singing males to the total number of birds in a population. This step also is fraught with problems not likely to be appreciated except by those engaged in intensive study of a species.

Since we usually find songbirds in pairs, we conveniently assume there are about as many females as males. Observers, however, commonly record more males then females but doubt this indicates an excess of males since they are more conspicuous. For example, in the Kirtland's Warbler unmated males are found occasionally, but unmated females are never seen. Are there no unmated females or are they just impossible to find?

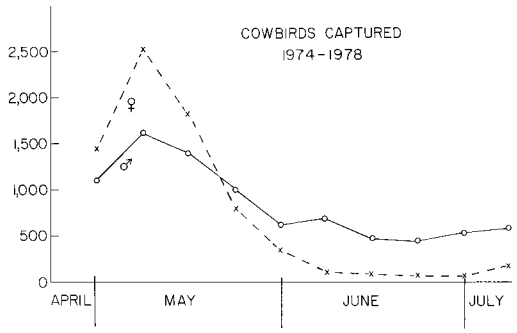

FIGURE 1. Points on chart show five-year totals for number of Brown-headed Cowbirds captured during each week of the breeding season in northern Lower Michigan.

Intuitively we expect females to be fewer than males because they are judged to be at greater risk sitting on nests than males flying freely. Indeed, in long-term studies of nesting populations, we often record higher survival rates for males, but we know also that males of some species are more likely to return to the same nesting site year after year, and thus more females survive than are counted.

The fact that nearly all males and females we see are mated and nesting is reassuring at first glance, but it leaves open the possibility some behave in a different way and do not conform to our assumptions. For example, how many yearlings breed and hold territories? We know that many yearling songbirds nest, but we find so few of them we cannot be sure all of them do so.

Among Prairie Warblers, Nolan (1978:359) did not find males outnumbering females. He found the apparent ratio changing as the season progressed, with females slightly outnumbering males during the height of the nesting season when all of the females were in breeding condition.

Sex ratios in Brown-headed Cowbirds vary widely as the season progresses, and observers have reached different opinions about the true sex ratio. I have analyzed a sample of 18,000 taken in five breeding seasons through trapping and removal of cowbirds in the Kirtland's Warbler nesting range (Shake and Mattsson 1975). This trapping came close to achieving the goal of the 100% sample, since it removed cowbirds so completely from the locality that we rarely saw this species outside the traps, and parasitism of Kirtland's Warbler nests dropped nearly to zero in most years.

The sex ratio changed by weeks in the five years, 1974–1978 (Fig. 1). In the total sample males outnumbered females by 22%. The ratio, however, varied greatly through the season and yet consistently from year to year. Clearly, males late in the season tended to move more than females into the vacuum created by trapping, and the variations may reflect differences in mobility rather than the true ratio of the sexes. In the first three weeks of each season, April 25 to May 14, females outnumbered males 5:3, but the ratio reversed in the last five weeks of the nesting season, June 5 to July 12, when males outnumbered females 4:1. These shifting ratios are difficult to interpret, even though the totals are comparable to those reported by other investigators using different methods in different regions, notably Darley (1971:563), who concluded males outnumbered females by 30–50%. These findings, with discrepancies of 30% or more, illustrate the uncertainties about sex ratios even among common and well-studied birds.

CONCLUSIONS

1. Censuses of singing males yield efficiencies below 50% for many species, and some common nesting birds cannot be censused effectively by the usual transect and spot-listening methods. Cuckoos and hummingbirds might head such a list, and woodpeckers also are candidates.

2. Singing behavior differs so much and sex ratios are so poorly known that generalizations from one species to another are untrustworthy, and the special problems with each species can be appraised adequately only after prolonged and detailed study of each.

3. People studying song and reproductive behavior should address themselves to the censusing problem and give informed judgments about the sources and magnitude of errors to be expected in standard methods of population counts.