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BIRD POPULATIONS CONSIST OF INDIVIDUALS DIFFERING IN MANY RESPECTS

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ABSTRACT.—Differences in the detectability of individual breeding pairs were analyzed, with special emphasis on least detectable birds. The mapping method was used to estimate numbers. The analysis is restricted to that part of the population whose nests had been located. It was found that the detectability of particular pairs ranged from less than three to almost ten records per ten visits. The proportion of least detectable birds depends on many interrelated factors, including habitat type, population density and breeding success. It also varies with time.

There is growing evidence that large differences exist among individual birds of the same population, and that these differences can play an important part in population processes responsible for stability (Dröscher 1974, Best 1977, Kuroda 1977, Payne and Payne 1977).

If so, it would be useful to recognize the nature of these differences, and to determine their range under various habitat conditions. I suggest that differences in the detectability (conspicuousness) of individual birds might be considered as one of the indices resulting from underlying behavioral or ecological factors varying between conspecifics within a given population. In this regard, it would be important to know whether clusters of few records (less than three per 8–12 visits when using the standard mapping method to estimate the density of breeding pairs) really represent surplus registrations, as suggested in the IBCC (1969) recommendations. Perhaps they represent special breeding bird categories, one of the characteristics of which is inconspicuousness to the observer. In this paper I attempt to shed some light on this problem.

That individual differences among birds are very large, and can have major effects on their detectability, was demonstrated when I observed the responses of Red-backed Shrikes (*Lanius collurio*) to nest inspection (B. Diehl, unpubl. data). At some nests there were no signs of the parents. They were, however, hidden not far from the nest. This became evident in a few cases when a nestling started to vocalize loudly when handled or touched; the parents revealed their presence at once. At the other extreme were those birds, both males and females, which attacked me vigorously as soon as I approached their nests. I could see and hear them at every nest inspection.

METHODS AND MATERIALS

The study was carried out on a meadow in Kampinos National Park near Warsaw, Poland. This meadow includes a mosaic of sites ranging from marshes with standing water more than 0.5 m deep in spring to dry sites submerged only after heavy rains. Clumps of trees, remnants of the forest cleared early in this century, are scattered throughout the area. The meadow had been grazed and mown up to the early 1960s, when a nature reserve was established. From that time the meadow has been in the first stages of forest succession with such trees as alders, willows, and birches the dominant plant species in the undergrowth.

Two adjacent plots, of 20.5 ha and 23 ha, were censused from 1964 to 1980 (the years 1966–1968 are excluded from the analysis because of an insufficient number of visits). On one plot clumps of trees and shrubs were more densely and more uniformly distributed than on the other, and this was reflected in the density of particular bird species.

The mapping method was used to estimate the number of breeding pairs. The number of visits per plot ranged from 19 in 1977 to 52 in 1964 (Table 1). They were generally made from late April to late July, although in some years they continued through August. Visits ranged from about three to four hours, sometimes five hours, early in the morning.

Adult birds were not individually marked, thus in the analysis of differences between individual pairs only those whose nests had been located were used. Due to this, it was possible to reduce the error that may occur when delimiting boundaries among clusters of registrations on the species maps, particularly with birds with few registrations that otherwise might be considered surplus birds. The number of nests located is shown in Table 1: only first broods are considered.

Since species detectability varies largely with the phase in the breeding cycle, four phenological periods have been distinguished, and most results are calculated for each of them separately. These are (1) the prelaying period, (2) the laying and incubation period, (3) the brooding period, and (4) the first two weeks after fledging. These periods were individually timed for each pair, and the number of censuses falling within each of these periods was then determined for each pair, the number of registrations on these censuses was then counted from the species map. The date of the first observation of any given bird was accepted as the date of its arrival from the wintering grounds. This could bias the results toward increased detectability indices in the prelaying period since some time could elapse between the actual date of arrival and the date of the first observation. Some birds were not registered at all over the prelaying period. In such cases an assumption was made that they were present in their territories at least one week preceding the onset

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TABLE 1
THE NUMBER OF CENSUSES AND BREEDING PAIRS WITH LOCATED NESTS IN PARTICULAR STUDY YEARS

		Number of pairs				
		Red-backed Shrike			Barred warbler	Icterine warbler
Year	Total number of visits per plot	Successful breeders	Unsuccessful breeders	Total	Successful breeders	Successful breeders
1964	52	12	9	21	2	0
1965	38	10	9	19	2	0
1969	31	13	5	18	12	0
1970	23	13	11	24	8	0
1971	28	13	17	30	5	2
1972	27	8	28	36	7	1
1973	28	16	10	26	5	0
1974	32	7	25	32	2	0
1975	23	10	16	26	7	0
1976	32	5	18	23	2	3
1977	19	10	14	24	6	4
1978	34	8	6	14	4	1
1979	32	1	13	14	5	1
1980	36	2	5	7	2	4
Total	435	128	186	314	69	16

of laying, and the number of censuses made during this period was used in further calculations for the prelaying period.

My visits were not evenly distributed over the breeding season, ranging from one to 14 for individual pairs in different phenological periods over all the study years. Thus the data for all years have been pooled to increase the reliability of the results, and an average number of registrations per breeding pair per 10 visits was calculated for each of the phenological periods. Also, the frequency distributions of birds differing in detectability were computed as mean values for all the study years.

This analysis was done only for successful breeders, as it is frequently impossible to precisely time phenological periods for unsuccessful breeders.

Three species are analyzed here: Red-backed Shrike, Barred Warbler (*Sylvia nisoris*), and Icterine Warbler (*Hippolais icterina*). All of them are late breeders, returning from migration either in the first half of May (Red-backed Shrike and Barred Warbler) or in the second half of May (Icterine Warbler). The four phenological periods total about two months.

The three species differ in their behavior. Red-backed Shrikes display very little vocal activity. They utter special vocalizations when establishing territorial boundaries, and thereafter are almost completely silent until the young fledge. Nevertheless, they are very conspicuous because, when hunting, they perch motionless on peripheral parts of shrubs at a height of 1–3 m and look for invertebrates moving in the grass around them. At that time they are well exposed to an observer, even over large distances, since the white-brown coloration of the male contrasts sharply with the background of green foliage. Consequently, this species was mostly recorded by sight. The other two species are typical song birds, and thus I primarily recorded singing males.

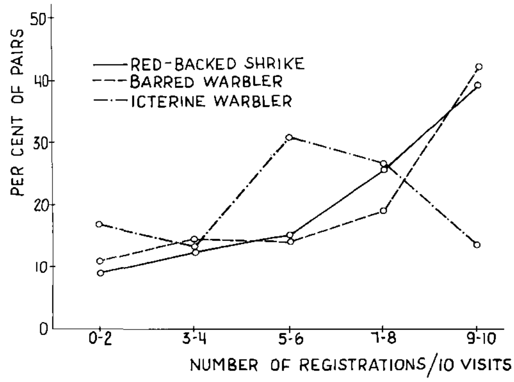

FIGURE 1. Frequency distribution of the detectability for successful breeders in the Red-backed Shrike, Barred Warbler and Icterine Warbler in the prelaying period (all the years pooled).

RESULTS

RANGE OF INDIVIDUAL DIFFERENCES IN DETECTABILITY

The frequency distribution of registrations for successful breeders in the prelaying period ranged from 0–10 records per 10 visits (Fig. 1). Between 10 and 20% of pairs had less than three registrations.

The proportion of birds with less than three registrations largely increased in the incubation, brooding and fledgling periods (Fig. 2), except for the Red-backed Shrike in the fledgling period.

These results suggest that at least some clusters of less than three registrations per 10 visits should not be considered as surplus ones. The number of such clusters tends to increase with time, thus it is advantageous to census these species in the prelaying period. The decrease observed for the Red-backed Shrike concerns only successful breeders, not unsuccessful ones (see below).

THE EFFECT OF BREEDING SUCCESS ON DETECTABILITY

Figure 3 shows the frequency distribution of registrations for successful and unsuccessful Red-backed Shrike breeders, calculated as an average for the whole breeding season. The proportion of birds with less than three registrations was about 40% for unsuccessful pairs, compared to 12% for successful ones. This proportion increased as the season advanced, reaching a peak of about 50% in the brooding and fledgling pe-

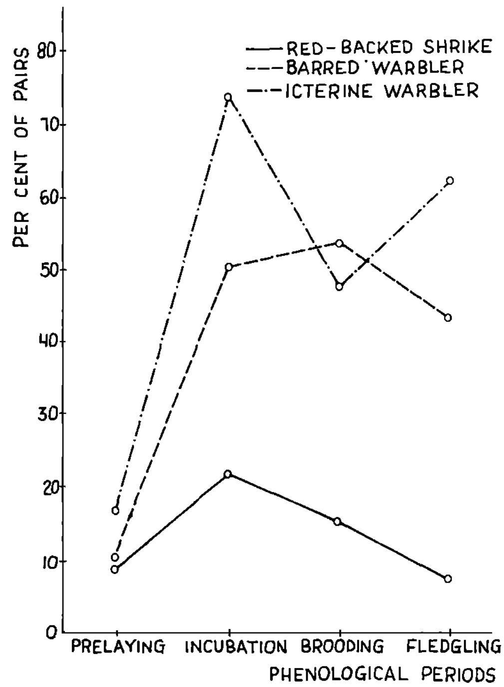

FIGURE 2. Frequency distribution of successful breeders with less than three records per 10 visits in four phenological periods (all the years pooled).

riods of successful breeders (Fig. 4). Thus individual differences in the conspicuousness of birds were additionally modified by their success at breeding.

The rate of brood mortality was density-dependent when a threshold population density was exceeded (Diehl 1976). For the Red-backed Shrike, this occurred on one of the study plots,

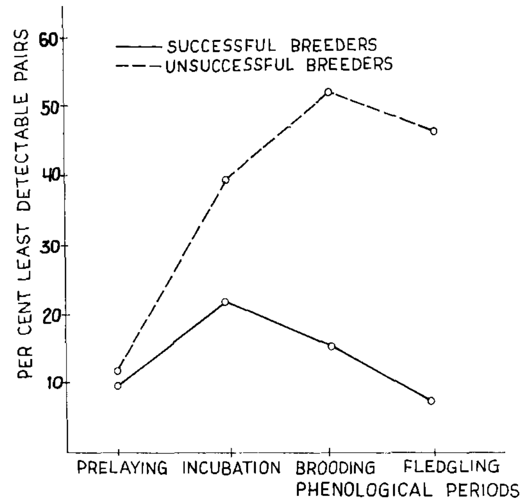

FIGURE 4. Frequency distribution of successful and unsuccessful Red-backed Shrike breeders with less than three records per 10 visits in four phenological periods (all the years pooled).

which I call the high-density plot. On the low-density plot, average shrike density was lower by half. Figure 5 shows the relationship between brood mortality and the proportion of low-detectable birds in the Red-backed Shrike population. Thus the danger of underestimating the population increases with growing population density as a result of increasing predation on broods, followed by changes in adult activity affecting their conspicuousness.

Weather conditions including air temperature also affect breeding success (Diehl 1976), with the same effects on the detectability of adults.

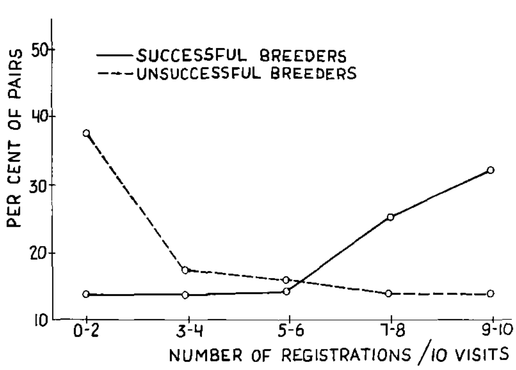

FIGURE 3. Frequency distribution of the detectability of successful and unsuccessful Red-backed Shrike breeders as an average for the whole breeding season (all the years pooled).

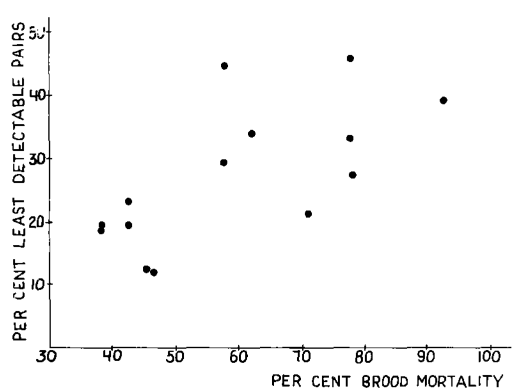

FIGURE 5. Scatter diagram of the proportion of breeding pairs with less than three registrations per 10 visits against brood mortality in the Red-backed Shrike in different years.

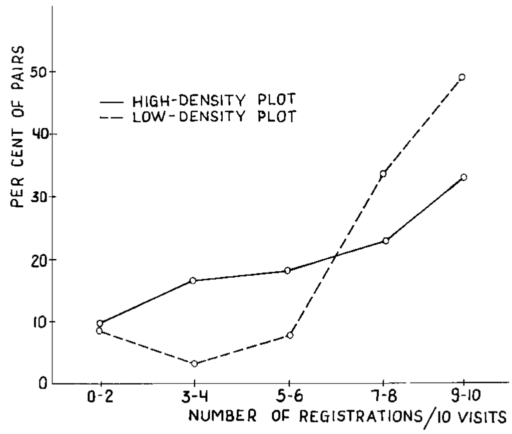

FIGURE 6. Frequency distribution of the detectability of successful breeders in the low- and high-density plots for the Red-backed Shrike in the prelaying period (all the years pooled).

Habitat-related Changes in Detectability

Apart from the differences in detectability related to breeding success, there were also differences within the group of successful breeders between the two plots. In the low-density plot the proportion of birds with few registrations was lower, and the proportion with a large number of registrations was greater, than in the high-density plot, particularly in the prelaying period (Fig. 6). As a result, shrike detectability was

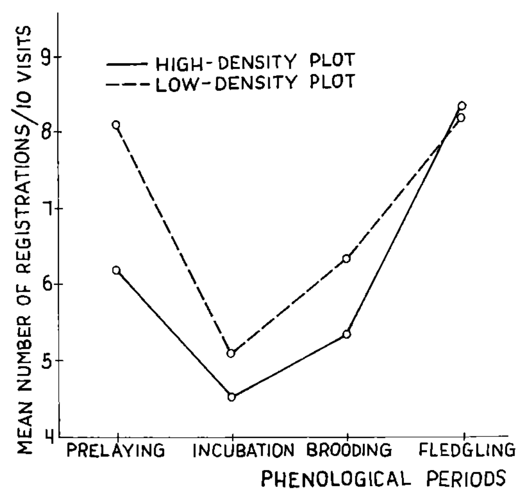

FIGURE 7. Mean detectability of successful breeders in the plots of low and high population density for individual pairs of the Red-backed Shrike in four phenological periods (all the years pooled).

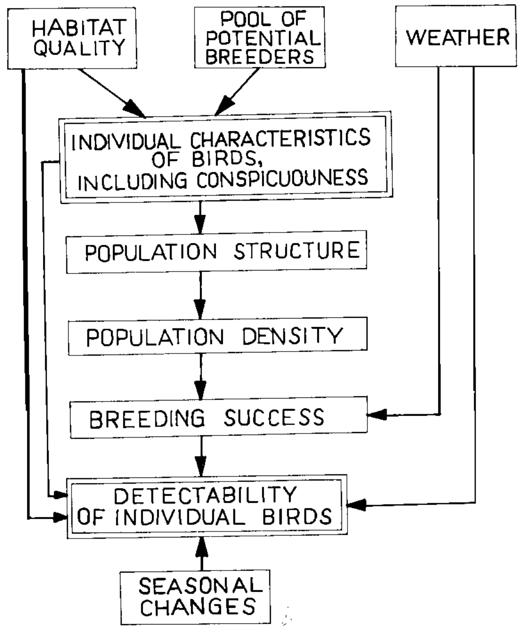

FIGURE 8. A scheme for the relation of individual variability to other factors influencing the detectability of birds in a population.

generally lower in the high-density plot compared with low-density plot (Fig. 7). This difference was most pronounced in the prelaying period (statistically significant at $P = 0.05$), then disappeared near the end of the breeding season.

The disappearance of this difference with time indicates that it is not simply related to habitat structure (more open in the low-density plot), instead, it suggests that there are some specific differences between the birds living in high and low densities. Again, the underestimation of population density as a result of rejecting clusters of less than three records can be greater in habitats with dense populations, at least for the Red-backed Shrike.

DISCUSSION

The present analysis reveals that there are large individual differences in the detectability of birds. Consequently, the effectiveness of the mapping method depends on the proportion of birds of various detectability in the population. The crucial point is the proportion of least detectable birds represented by clusters usually considered as surplus registrations. It can be very high during some periods in the breeding season. It does not seem possible to estimate their number without a greatly increased field effort. Is it worthwhile? The answer may vary depending on the purpose of the study. I would say yes if one wants to get a deeper insight into population processes.

The matter would probably be easier to cope with if we knew what other avian characteristics are associated with conspicuousness. In small mammals, for instance, individuals showing low trappability have low social rank, and are usually young (Gliwicz 1970). To my knowledge nothing of this kind is known for inconspicuous birds. There are, however, indications that great differences can exist between birds living in high and low densities. For instance, Red-backed Shrike males occupying the low-density plot were generally slightly less aggressive in response to the presence of an observer at their nests than those living in the high-density plot. Females were much more aggressive on the low-density plot (B. Diehl, unpubl. data). No correlation was found, however, between the aggressiveness and the detectability of those birds.

To characterize the possible importance of individual variation between birds to census efficiency against the background of other, usually interrelated factors, I propose a scheme in which this variability is an inherent component of the population structure (Fig. 8).