THE USEFULNESS OF ABSOLUTE ("CENSUS") AND RELATIVE ("SAMPLING" OR "INDEX") MEASURES OF ABUNDANCE

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ABSTRACT.—Territory mapping provides an estimate of density through repeated visits to an area, which lowers the chance of any resident birds being missed, but the usual estimate of the chance is obtained by circular reasoning, obscuring a severe bias for the less conspicuous species. Comparison with more detailed studies shows that territory mapping, point counts, and transect counts usually provide poor estimates of density. Given this, the Finnish technique of estimating density from transect counts of birds within and outside of an inner zone provides a useful compromise. For an index of density, point or transect counts are preferred because they can be applied to a wider range of species and seasons and seem more cost effective than territory mapping.

This paper compares the cost effectiveness of point, transect and territory mapping techniques for measuring absolute density and deriving indices of abundance. In another paper in this symposium I review various influences that affect the accuracy of point and transect counts. Here I first review territory mapping techniques in the same way, and then compare techniques in practical use.

INFLUENCES ON TERRITORY MAPPING

Territory or spot mapping techniques use data from several visits to a plot, on each of which the activity of each bird is recorded on a map. When the records of one species from all the visits are brought together, the information falls more or less easily into clusters corresponding to the territories of that species (Anonymous 1969, Enemar 1959, Williams 1936, Williamson 1964). The reasoning behind the method is that, if a bird has a probability q of not being counted on any one visit, this is reduced to q^n for n visits. If the value of n is high enough, very few territorial birds are missed.

In practice, one record is not enough to identify a territory; Svensson (1979a) recommends at least three 'registrations,' and shows that if q is less than about 0.5 the usually recommended number of 8–10 visits will reveal 90% or more of the clusters. When q is higher than 0.5, too many territories are missed. Accepting only two or one registrations as sufficient would allow more "territories" to be recognized, but would increase the risk of including chance clusters that do not correspond with territories. Increasing the number of visits is not an efficient way of identifying more territories of cryptic species, as the return per unit effort is small (for example, 16 visits are needed to identify 90% of territories if q is 0.7, and 52 visits are needed if q is 0.9). Territory mapping can therefore give an acceptable approximation to the true density

with an acceptable amount of work only if the probability of detecting a bird each visit is high.

Estimates of q in the literature (DesGranges 1980, Enemar et al. 1978, Hogstad 1967, Seierstad et al. 1970, Slagsvold 1973c, Svensson 1978a, Williamson 1964) are bedevilled with circular reasoning: clusters are identified and are equated with territories, and q is then calculated from the number of visits without records in each "territory," divided by the total number of visits. If territories of birds with a high value of q are not recognized or are merged, q will be underestimated. Whatever the value of q, some territories will by chance have too few registrations to be recognized. This also underestimates q (Järvinen and Lokki 1978). The underestimation is by 0.05 at $q = 0.6$ and 10 visits and becomes rapidly worse as q increases. Thus, when the probability of missing a species on any one visit is high, good estimates can be obtained only from independent and thorough density estimates, such as from intensively studied color-ringed birds (Snow 1965).

The probability of missing a bird will also vary with season as well as with the age, reproductive, or physiological state of the bird (Slagsvold 1973c) and with other factors such as habitat, time of day, or weather (Dawson 1981a). Seierstad et al. (1970) and Slagsvold (1973c) tried with some success to overcome some of these problems by estimating q separately for each segment of the population, but the technique lacks rigor and, as Svensson (1979a) pointed out, there is rarely enough information from any one mapping "census" (8–10 visits) to give a good estimate of q. Without good estimates of q, the equation of map clusters with territories remains uncertain.

Other problems in estimating density from maps arise from the difficulty of identifying clusters and of allocating edge clusters. Best (1975) and Svensson (1974b) found considerable variation between different people's interpretation of species maps: coefficients of variation ranged from 15 to 36 for territorial passerines. Keeping

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the same observers and standardizing the rules used for interpretation will remove some, but not all, of this variation.

That these problems may greatly influence the 'densities' estimated for most species is shown by studies comparing mapping results with more detailed studies (Bell et al. 1973, Diehl 1974, Enemar et al. 1978, Haukioja 1968, Jensen 1974, Mackowicz 1977, Mannes and Alpers 1975, Nilsson 1977b, Snow 1965). For a minority of species surveyed at the right time, the mapping method may yield a good density estimate, but in general it gives an index, not an estimate, of density.

Three studies where different observers were used in the same areas provide information on the precision of the mapping method as an index of numbers. I use the mean-to-variance (between observers) ratio as a measure of repeatability. Snow (1965) found large differences between farmland species, some (e.g., the Blackbird, *Turdus merula*) having means much less than the variance between observers and others (e.g., the Great Tit, *Parus major*) the converse. However, Frochot et al. (1977) and Enemar et al. (1978), confining their attention to small passerines in forest, found means almost always greater than variances. More work is needed to confirm this hint that mapping in forests may give an index of numbers that is quite insensitive to a change of observer.

THE STATISTICAL BEHAVIOUR OF THE COUNTS

POINT COUNTS COMPARED WITH TRANSECTS

Järvinen (1978a) considered line transects to be superior to point counts in two respects. The average distance of detection in a line transect is linearly related to the effective area sampled, but in point counts the area is proportional to the square of the distance. This means that the same size of error in judging distance has a greater effect on density estimates from point counts than on those from transects; Emlen (1977a) suggested that distance estimation is facilitated in transect counts by the possibility of hearing a bird from a length of trail and thus getting a better 'fix' on it. Table 1 compares the repeatability (standard deviation) of estimates of distance for point counts and transects from the same areas; neither technique seems uniformly the more accurate, so one might prefer transects. Imprecision in distance estimates is a problem only if an estimate of area is needed to convert counts into densities.

Järvinen's second point was that the "saturation effect" (more cues being missed when there were more birds recorded in total) was not important in line transects. However, his evi-

TABLE 1
A COMPARISON OF DISTANCE ESTIMATION IN POINT AND TRANSECT COUNTS (TRANSECT RESULTS IN BRACKETS)

Species	Average percentage "Far" Records[a]	Standard deviation of the average[b]
Blackbird (*Turdus merula*)	50 (22)	12 (12)
Goldfinch (*Carduelis carduelis*)	45 (25)	3.3 (9)
Myna (*Acridotheres tristis*)	76 (58)	8 (6)
Skylark (*Alauda arvensis*)	56 (28)	16 (3)

[a] Data from 200-m transects and 5-minute point counts made in pastoral land in Hawke's Bay, New Zealand, March 1980.

[b] The standard deviation is of four estimates of the percentage, one for each day of the study and each based on 96 five-minute point counts or 80 transects. The variance of the percentages differs significantly only for the Skylark ($P < 0.05$ in F tests).

dence for this (Järvinen et al. 1978a, 1978b) is indirect, and the conclusion seems unlikely. Ramsey et al. (In press) preferred point counts to transects; they held that transects miss more of the birds close to the observers, but they did not state how they knew this.

Dawson and Bull (1975) compared the results obtained in point counts and transects (0.7 km/ h) in the same area. Their analysis was of the total counted as an index of density and showed that the two techniques were of similar value for demonstrating differences in mean values of the count. Subsequent more extensive work in pastoral and orchard land has supported this conclusion (Dawson and Robertson, unpubl.). Dawson and Bull (1975), Källandar et al. (1977), and Ramsey and Scott (1979) preferred point counts for work in forests because this method allowed undivided attention to be given to the birds and was probably much less affected by variation in terrain.

Ratowsky and Ratowsky (1979), working in Tasmanian forests, detected more species in 5 min walking at 3–6 km/h than in 5 min standing. Dawson and Robertson (unpubl.) have found the same in New Zealand farmland. Thus, if the main aim of the survey is to acquire a species list quickly, transect counts may be preferred.

Yapp (1956) examined the theoretical relationship between the speed of the observer, w, and of the bird, u, and the coefficient for converting counts into densities, k. His model is that $k \propto (u^2 + w^2)^{-\frac{1}{2}}$. It is not valid for point counts ($w = 0$) because it deals with the entry of new birds into the observer's range, not with those initially there (Skellam 1958). For the same reason it will overestimate the density if the transect is short relative to the "effective radius" (Yapp 1956) of the birds. The effect of observer speed needs further study, and other effects might be ex-

pected—for example an observer will make more noise if he walks faster.

ESTIMATION OF DENSITIES IN POINT AND TRANSECT COUNTS

Four approaches have been used to convert counts, c, into estimates of density, d. In the first, an independent "census" method is used to establish densities in the same places that counts are done, and k is estimated from $k = d/c$ (Ferry 1974, Gill 1980, Walankiewicz 1977). Given all the possible influences on k that I have discussed elsewhere in this symposium, such a calibration would be needed for a range of conditions, and can be no more than approximate without a prodigious amount of work. However, the small differences in k between habitats found by Gill (1980) give some hope. Of course, the usefulness of such estimates of k also depends on the accuracy of the independent estimate of density—a point discussed with regard to a mapping "census" in the first part of this paper.

The second approach is to collect information on the distance of detection of each bird and to establish for each species a distance up to which all individuals are detected (the "basal radius" of Ramsey and Scott 1979, see also the "specific strip" of Emlen 1977a and Balph et al. 1977). The records beyond this distance can then be discarded and the population estimate based upon those within the distance. Ramsey and Scott (1979) discuss criteria for estimating the basal radius, and it is clear that even their best method is subject to considerable bias and imprecision. Another problem with this technique is that it may necessitate discarding most of the records of some species, so that the density is based upon a small count.

The third method is to use the distribution of detection distances to give an estimate of a single effective distance, r: this is the "effective radius of detection" of Ramsey and Scott (1979), which is directly related to the effective area sampled and to my k by the equations $k = 1/\pi r^2$ for point counts, and $k = 1/r\,l$, where l is the length of a line transect. These equations permit density to be estimated from the total count. Ramsey and Scott (1979) estimated r via their basal radius r_b: $r = r_b(n_b/n)^{-\frac{1}{2}}$, where n_b is the basal number detected and n is the total number detected. This is subject to the same problems as their basal radius (see above) with an added error introduced in the conversion. J. T. Emlen (1971) estimated $1/k$ (his "coeffecient of detectability") by using a maximum count in bands close to the observer to estimate the number that there should have been in a wider band; the fraction of this estimated number that was actually

counted gave his coefficient. Nilsson (1974a) attempted to get an independent estimate of the "effective radius of the birds" of Yapp (1956) using Brewer's (1972) method of estimating the "distance at which the number of near birds missed is equal to the number of far birds observed." However, this method too assumes that all the birds are observed in a band close to the observer and is therefore Emlen's technique in another form, so the close agreement between the two methods is no confirmation of either's accuracy. As both techniques depend on a basal density, they have similar problems to Ramsey and Scott's (1979) technique.

Järvinen and Väisänen (1975) described methods of estimating r in which the observations were simply classified into those within a main belt and the remainder. They used three models for the impairment of detectability with distance—exponential, linear, and half-normal—and found that their estimate of k differed little between the models, except when far records were less than 50% of the total. Most of their species had 60–90% far records (outside the 25 m inner belt they used) and for these their linear model estimator $r = w/(1 - f^{\frac{1}{2}})$, where w is the width of the near belt and f is the proportion of records that were far, is a reasonable approximation. There should be no great problem in applying similar reasoning to point counts.

The fourth method is to use the distribution of detection distances to give an estimate of density close to transect lines. Provided the lines are placed so as to sample the area randomly, this density will be representative. Burnham et al. (1980) give an excellent review of such methods.

The methods that use estimates of detection distances share several problems (see also Ramsey et al. 1979 and Burham et al. 1980).

1. Not all birds may be detected, even in the area close to the observer. My experience of counting birds in New Zealand native evergreen forests has provided plenty of anecdotal evidence that birds may easily be missed even when overhead. Emlen (1977a) tried to overcome this problem for breeding birds by estimating "cue frequency" of singing males in a similar way to the "efficiency" (q) of a mapping census, a technique that also has problems (see the first section of this paper). No one has suggested what to do about the near birds missed outside the breeding season.

2. Estimates of distance may be imprecise and biased, especially when they are based on a distant sound. I have found no published study of this fundamental problem, but Ramsey and Scott (1979), in estimating k for each observer, admitted its importance. Table 2 examines the

TABLE 2

THE DIFFERENCES BETWEEN FOUR OBSERVERS' ESTIMATION OF DISTANCE, AS SHOWN BY THE PERCENTAGE OF "FAR" RECORDS[a]

Species	Observer							
	A		B		C		D	
	Total	% far	Total	% far	Total	% far	Total	% far
Goldfinch	263	60	294	64	271	22	171	28
Blackbird	46	74	28	29	37	43	31	45
Myna	147	86	175	85	133	68	109	56
Skylark	82	72	60	77	74	35	63	40
All four	538	70	557	70	515	37	374	40

[a] From 96 five-minute counts by each observer in the study described in Table 1. There was a highly significant difference in the percentage of "far" records between the four observers for all four bird species ($P < 0.01$ in chi-squared tests). Small samples could account for some of the variation in the percentages (especially the low value for the blackbirds by observer B) but clearly the most important factor is a difference between the four observers' perception of distance.

difference between four New Zealand observers' estimation of the proportion of birds beyond 50 m, and suggests that the problem is significant.

3. The birds may react to the observer in such a way as to either increase or decrease the numbers detected close by, and so violate the assumption implicit in all techniques, that the observer has no influence on the probability of detection. Some published detection curves are suggestive of a movement away from the observer (e.g., Nuthatch, *Sitta europaea*, Nilsson 1974a, table I plot II; Wren, *Troglodytes troglodytes*, Hope Jones 1974), and a small amount of movement will not be obvious, but will still bias the estimate.

4. The birds may move into or out of the observer's range through their natural activity; none of the models allows for the movement of birds.

5. Estimates of r will be needed for all combinations of factors that I have shown elsewhere in this symposium to influence k, otherwise these factors must be held constant or a very robust estimator used (Burnham et al. 1980). Ramsey and Scott (1979) allow for k to vary with observer, habitat, and species, and standardized season, time of day, weather, and noise (J. M. Scott pers. comm.).

Attempts have been made to validate some estimates of k through independent estimation of densities. Emlen (1977a) compared densities obtained by his cue-frequency method with the mapping-method densities, but in fact his cue frequencies came from those same mapped territories and so were not independent. Järvinen et al. (1978a) in Lapland, and Järvinen et al. (1978b) in Poland compared the Finnish line transect with mapping, and Franzreb (1976) compared J. T. Emlen's (1971) technique with mapping. All three comparisons showed that the two techniques correlated well, with the tran-

sects usually giving slightly lower "densities" than mapping, but both approaches have their problems. Suffice it to say here that Järvinen and Väisänen's (1975) simple linear model may be as accurate as any, given the many possible sources of error. If one could be confident the errors were small, Burnham et al. (1980) offer a good range of transect techniques to choose from and a modification of Ramsey and Scott's (1979) point count method.

THE CHOICE OF TECHNIQUE

Territory mapping is normally suitable only for counting the stationary part of noncolonial passerine bird populations during the breeding season (Anonymous 1969), but transect or point counts are suitable for a wider range of species and seasons. If the problem being investigated requires estimates of density, none of the techniques reviewed in this paper can give an accurate answer for most species. More work is needed comparing these simple techniques with good estimates of density acquired from intensive study of marked populations, as most of the work to date has compared one imperfect measure with another. In the meantime, estimates of "density"—whether acquired from territory maps or from conversion of index counts—must be considered as subject to large and unknown errors. Many studies have assumed to the contrary, and without evidence, that territory mapping provides a good estimate of density (DesGranges 1980, Głowaciński and Weiner 1977, Walankiewicz 1977, Williamson 1964). Transects may be preferable to point counts when estimating density, as errors in calculating the effective area sampled are less, and a species list is acquired more quickly. Nevertheless, point counts are preferable in difficult terrain.

If the question being asked requires only an index of density, the choice depends on which technique has the lowest variability (Dawson

and Bull 1975, Enemar et al. 1978). I have already concluded above that point and transect counts are about equally good on these grounds. Enemar et al. (1978) compared an index of abundance based on territory mapping with the total number of contacts achieved in the same study, and concluded that the two approaches were equally good. However, a territory-mapping survey is probably not the most efficient way of obtaining contacts. For example, in 8–10 two-hour visits to a study area using the point-counting technique of Dawson and Bull (1975), Dawson et al. (1978) acquired over 100 contacts for five species, whereas Enemar et al. (1978) averaged over 100 for only one species. If the point counts fit a Poisson distribution and are subject to a square root transformation to bring the variance to approximately 0.25, the mean count of four observers will have a standard error of about 0.025, or 1–3% of the mean for common species, but four mapping censuses would give standard errors at least 6–20% of the mean (Enemar et al. 1978, Snow 1965). Thus, point and transect counts seem to give a more cost-effective index of density than does territory mapping; it is a pity that there has been no direct comparison of the techniques to confirm this conclusion.

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