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PLOT MAPPING: ESTIMATING DENSITIES OF BREEDING BIRD TERRITORIES BY COMBINING SPOT MAPPING AND TRANSECT TECHNIQUES

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ABSTRACT.—Originally proposed by J. T. Emlen in 1977, plot mapping combines the accuracy of territory or "spot" mapping with the efficiency of transect or plot count techniques. This method can be used to estimate densities of animal species that advertise their presence on mutually-exclusive territories. Plot mapping can be used with transects or sample plots, with fixed boundaries or species-specific variable boundaries. It is especially well-suited for censusing breeding songbird communities. For each species, a probability of detection is estimated and subsequently used to adjust song counts to territories present. The variance of the density estimate provides a measure of its precision.

Estimating densities of territories of breeding birds based on counts of singing individuals is confounded by sources of error that may be grouped into two categories: (1) unknown rates of sound attenuation with increasing distance from the observer, and (2) unknown and varying rates of singing by the bird. Methods that have been proposed for dealing with the first type of error (Emlen 1971, Burnham et al. 1980, etc.) involve mathematical relationships between sound attenuation and distance for variable-width transects and variable-radius circular plots. The problem can be circumvented, however, by choosing a strip transect width (or circular plot radius) small enough that the probability of detecting a singing bird is always equal to one. Such narrow fixed-width strips and fixed-radius circular plots require only that the observer determine whether or not the detected bird is within the sample area.

Emlen (1977) has been the only one to address the second source of error: birds do not sing all the time. The probability of detecting a territorial bird even nearby is not equal to one if the bird is silent and inactive; in some habitats, in fact, that probability may be zero. Any methodology that fails to account for undetected territories will consistently underestimate densities.

Emlen (1977) proposed a simple intuitive method for estimating territory densities from song detections, which entailed calculating an instantaneous sound detection frequency and then using it to adjust the density estimate for territories that were not detected. The method is applicable to both variable- and fixed-distance survey techniques. Surprisingly, Emlen's method has received little attention from field researchers and apparently even less from theoretical biometricians. In a recent symposium devoted entirely to counting birds (Ralph and Scott 1981), few participants acknowledged Emlen's (1977) technique for dealing with nondetected birds at short distances, and only one (Tilghman and Rusch 1981:202) reported ever having used the method. My purpose here is to describe an expansion of Emlen's technique, report on its application, and encourage its use and evaluation in the field.

I have tried to quantify density of **territories** rather than density of individual birds because (1) density of territories probably depends upon habitat quality (which is often what one wishes to study), (2) density of territories is probably constant throughout a breeding season in spite of mortality, as the frequently observed, almost immediate reoccupation of abandoned territories seems to suggest, and (3) some territorial pairs may have helpers, confusing the numerical relationship between singing males and individuals.

THE THEORY

A male songbird's frequency (cues per unit time) of singing depends on the species, its population density, the time of day, the stage in the breeding season, the habitat, and individual variation in behavior. The probability that such a bird will be detected by its song depends on how often the bird is on its territory, the frequency of singing, the length of time the observer is within potential detection distance, and observer sensitivity. All of these factors contribute to an actual, observed frequency of detection that will seldom be equal to one (Emlen 1977; Diehl 1981; Emlen, pers. comm.). However, if a transect or circular plot were censused x times and a singing bird detected in approximately the same location y times, we could assume that this was the same individual on his territory and the frequency of detection was y/x. The fraction thus derived simultaneously describes the biological components of singing frequency and the human components of song detection. Suppose that a strip transect were traversed 10 times, and inspection of the composite plot map revealed three clusters of Carolina Wren (*Thryothorus ludovicianus*) song detections, one consisting of 4, one of 5, and a cluster of 6 song detections. The mean frequency of detections (=probability of detection) would be therefore 5/10. At this time and place, Carolina Wrens would have been detected by song 5/10 of the time.

The empirically derived, instantaneous frequency of detection is species-, space-, time-, and even individual-specific. Nevertheless, the mean of several individual frequencies of detection (i.e., the probability of detection) calculated for a single species at one place and time could be used to adjust detected songs at that place and time to actual territories present.

The density of territories is estimated by dividing the probability of detection into the mean number of detections per replicate within the sample area as defined by the pre-determined fixed distance or the species-specific variable distance. Where $P(d)$ is the probability of detection and $\bar{d}$ is the mean number of detections per replicate, the density of territories actually present may be given as: $\hat{D} = \bar{d}/P(d)$. Returning to the Carolina Wren example, suppose the 10 traversals of the strip transect resulted in a mean of 2.0 song detections per traversal. We have already estimated the probability of detection as 5/10, therefore, 2.0/(5/10) = 4.0 Carolina Wren territories are present.

All detections within a presumed territory must be used to calculate the frequency of detection, even if some lie outside the fixed boundaries (when applicable) of the sample plot. On the other hand, territories that are suspected of extending beyond the observer's range of detection should not be used in the calculation of the probability of detection because such $P(d)$s will be too low if the observer fails to hear a bird singing on the most distant part of its territory. Of course the mean number of detections per replicate will always include only those detections from within the sample plot of known area.

Because they are both means, the probability of detection ($P(d)$) and the mean number of detections per replicate ($\bar{d}$) may have measures of precision associated with them. Although it is rarely done, I believe it would be desirable to express density estimates with a variance or standard deviation that would serve as an index of the precision of the density estimate. Unfortunately, estimating a measure of precision for the ratio of two means requires a knowledge of their covariance, and estimating the covariance for non-paired samples is not possible. This problem can be avoided, however, by first using multiple sample plots and calculating the mean number of detections per replicate on one plot and then dividing that value by the probability of detection estimated from the remaining sample plots. Density estimates for each of the sample plots are then calculated with the $\bar{d}$ of that plot and a $P(d)$ from all the other plots. Since the two components of the ratio are independent (calculated from different sample plots), they may be assumed to have a covariance of zero, and methods for division of such means and their variances are available. The approximate variance of the ratio of two random variables with zero covariance is given as (Mood et al. 1974: 181):

$$\mathrm{VAR}\left(\frac{x}{y}\right) \approx \left[\frac{\mu_x}{\mu_y}\right]^2 \cdot \left[\frac{\mathrm{VAR}(\mu_x)}{\mu_x^2} + \frac{\mathrm{VAR}(\mu_y)}{\mu_y^2}\right]$$

where μ_x and μ_y are the mean number of detections per replicate and the probability of detection, respectively.

THE APPLICATION

I attempted to estimate densities of 30 species of territorial singing birds on the White River National Wildlife Refuge in the Mississippi Delta of eastern Arkansas. The habitat was mature bottomland hardwood oak-hickory forest with a dense understory and a partially closed canopy. Visibility in this habitat is severely restricted and I was practically limited to counts of singing birds. Survey work was conducted in May and June 1980 between daybreak and 4 h after sunrise, and limited to rain-free mornings. I established and surveyed 39 strip transects, each 500 m long with a fixed width of 100 m (5 ha).

Moving at about 1 km per hour (the actual speed of traverse is not important, but it must not vary between replicates, lest the observer remain within detection distances for varying lengths of time), I recorded the approximate position of singing birds relative to the center line. Although I seldom actually saw a singing bird, I was usually able to determine the tree or bush where it was perched. I recorded the species, the position along the transect, and the estimated perpendicular distance to the bird from the transect center line. I also recorded visual sightings, call notes, and simultaneous singing by two or more individuals of the same species. I noted all birds detected even if they were beyond the 50 m fixed width. It took 25 to 35 min to walk a transect and each was repeated 6 to 10 times over as brief a period as possible, the complete survey of a single transect never requiring more than five days. Each species was plotted on a separate strip of graph paper (scale 1:1950) for each transect with all traversals on the same strip.

Plot maps for the Acadian Flycatcher (*Empidonax virescens*) on transects WA-29 and WA-30 are provided as an example (Fig. 1). Three distinct clusters of song registrations are evident on WA-29 and two clusters on WA-30. I assumed each of these to represent a single territory with observed frequencies of detection of 6/7, 5/7, 6/7, 4/7, and 6/7. Registrations B, C, D, and G near 300 on WA-29 might have been considered a cluster, but because of ambiguous interpretation (should A be included?), I chose not to include this cluster. Interpretation of the group of registration points at the bottom of WA-30 also proved to be difficult, and so no territories were recognized there. Nevertheless, five clearly-defined territories were available for the calculation of the probability of detection. The mean of the five frequencies of detection is the probability of detection: $P(d) = .7714$; VAR $= .0163$.

The seven traversals of WA-31 (not figured) yielded a mean ($\bar{d}$) of 2.714 (VAR = .5714) Acadian Flycatcher song detections per traversal. The estimated density of Acadian Flycatcher territories on WA-31 was therefore:

$$\hat{D} = \frac{\bar{d}}{P(d)} = \frac{2.714}{.7714} = 3.52\frac{\text{territories}}{5\text{ ha}},$$

and the variance is approximately:

$$\left[\frac{\bar{d}}{P(d)}\right]^2\left[\frac{\text{VAR}(d)}{\bar{d}^2} + \frac{\text{VAR }P(d)}{P(d)^2}\right]$$

$$= \left[\frac{2.714}{.7714}\right]^2\left[\frac{.5714}{(2.714)^2}\ \frac{.0163}{(.7714)^2}\right] = 1.299.$$

To express the density and its variance in territories/ha, the density in territories/5 ha is divided by 5 and the variance is divided by 5^2 (= 25):

$$\hat{D} = 3.52/5 = 0.704 \text{ territories/ha}$$

$$\text{VAR}(\hat{D}) = 1.299/25 = .0502.$$

In order to estimate the density and its variance for the flycatchers on WA-29, I would use a $P(d)$ calculated from transects on WA-30 and WA-31, and so forth.

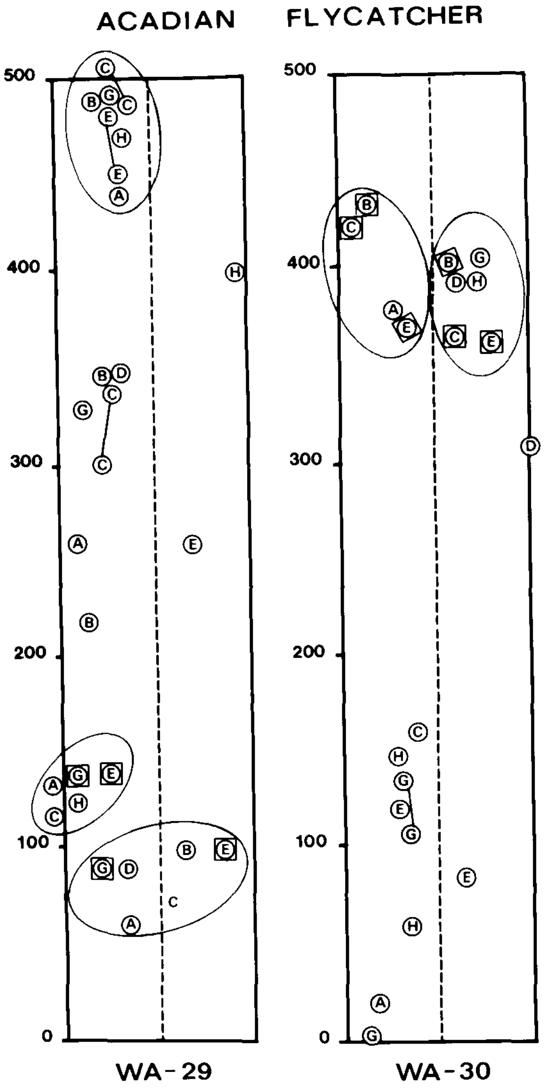

FIGURE 1. Plot maps from transects WA-29 and WA-30, White River National Wildlife Refuge, Arkansas, for the Acadian Flycatcher. The letters A, B, C, D, E, G, H represent seven separate traversals of the transects; F is reserved for sightings of females. A simple letter is a sighting or call note; a circled letter is a singing bird; circled letters within squares (always in sets of two or more) represent simultaneous song detections; a line between letters means the bird moved while I was observing it. The elipses circumscribe detections that are assumed to represent repeated detections of the same bird on his territory.

DISCUSSION

The method described here and originally by Emlen (1977) is simply a combination of spot mapping and transect techniques: spot mapping is used to calibrate transect (or circular plot) data. Many authors (e.g., Davis 1965, Svensson 1974, Best 1975, Oelke 1981) have pointed out the limitations and sources of error inherent in spot-mapping procedures. The most serious problem with spot mapping lies in the interpretation of the species maps and the delineation of territories from the plotted song registrations (Svensson 1974). The spot mapper is forced to make decisions on all clusters of plotted song detections, regardless of the difficulty and subjectivity involved in doing so. In plot mapping, however, one is not obliged to assign all song registrations to territorial clusters. In fact, clusters of registrations that are questionable and not clearly identifiable as individual territories should not be included in the calculation of the probability of detection. Thus, the most serious weakness of the spot mapping method does not apply to plot mapping.

Tilghman and Rusch (1981) compared the results of plot mapping (their "Emlen II" method) and 11 other transect techniques to spot mapping for 10 species of breeding woodlot birds in Wisconsin. They assumed that spot mapping provided their best density estimates, and calculated the absolute relative bias ($100 \times |\hat{D}_i - D|/D$, where D is the spot mapping estimate and D_i the mean estimate of bird density from the ith transect method) of each transect method for each bird species. They concluded that no one method provided the least biased density estimates for every species and that none of the methods tested was substantially better than the others. Because Tilghman and Rusch (1981) were unable to calculate song detection frequencies (i.e., probabilities of detection) for 3 of the 10 species (Eastern Kingbird, *Tyrannus tyrannus*; Black-capped Chickadee, *Parus atricapillus*; and White-breasted Nuthatch, *Sitta carolinensis*), they omitted this parameter from their density calculations for these species (N. Tilghman, pers. comm.). Common Yellowthroat (*Geothlypis trichas*) density was estimated with the probability of detection calculated from a 10-visit spot map, and the number of songs detected on a single traversal of the transect (N. Tilghman, pers. comm.). I recalculated the relative bias of each of the 12 transect methods for the six species with adequate data. The average absolute bias for the plot mapping method was 24%, whereas the average of all 12 methods was 40%, and the range was 21 to 62%. Only the transect method of Gates (1969) had a lower average absolute relative bias (21%) than the plot mapping method of Emlen (1977).

I attempted to census by plot-mapping 30 species of birds on 39 transects in the bottomland hardwoods of eastern Arkansas but was able to estimate detection probabilities for only 22. My failures were due to my inability to recognize enough discrete clusters (i.e., territories) among the plotted song detections. A species may have been too abundant (e.g., Blue-gray Gnatcatcher, *Polioptila caerulea*), or too mobile, or the territories were too large (e.g., Yellow-billed Cuckoo, *Coccyzus americanus*). These are, of course, problems inherent in the mapping method (Robbins 1978).

The most serious problem with the plot mapping is the potential to overestimate the probability of detection if sparse clusters are not recognized as clusters. A territorial bird that was detected only once in seven traversals would not be recognized as a cluster, and the actual observed frequency of detection of 1/7 would therefore not be included in the calculation of $P(d)$. Although the bias is always upward and the tendency therefore to underestimate densities, methods which wrongly assume a $P(d)$ equal to one at plot center will always underestimate densities by an even greater amount. Of course a territorial bird that never sings during any of the traversals will always be overlooked by any aural method.

Because frequency of singing varies with so many biological and environmental factors, probabilities of detection may not have general applicability and should probably be recalculated for each species, place, and time (but see Emlen and DeJong 1981). Nevertheless, if these variables are held as constant as possible, the variation in detection frequencies (and the variance of $P(d)$) should be minimized.

Despite its shortcomings, the spot mapping method is considered by most researchers to be the best tool available for estimating breeding bird densities (Robbins 1978). Used by itself, spot mapping is time-consuming whereas simple transect or circular plot surveys are not very accurate. Plot mapping, described here, attempts to combine the efficiency of transect or circular plot techniques with the accuracy of spot mapping.

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RECENT PUBLICATION

Birds of Prey of Southern Africa/Their Identification and Life Histories.—Peter Steyn, illustrated by Graeme Arnot. 1982. David Phillip, Cape Town and Johannesburg. 309 p. $39.50. Source: Buteo Books, P.O. Box 481, Vermillion, SD 57069. This slightly larger-than-field-guide size book presents in a useful form an abundant coverage of raptor field observations in southern Africa, which here includes not only the Republic of South Africa but also Namibia, Botswana, Zimbabwe and Mozambique as well as the southern parts of Angola and Zambia. Steyn did most of his field work in Zimbabwe and South Africa but with excursions into Namibia and Botswana.

Arnot's color plates are remarkably fine; more than just illustration, they are artistically painted with meticulous attention to detail. This is a considerable feat, for the 24 plates depicting 68 species of diurnal raptors and 12 owls have some 280 separate figures, often four of each species (adult and immature, perched and flying, and such aberrants as melanistic or pale forms). There are only two figures of the Banded Snake Eagle and Yellow-billed Kite, but seven of the Steppe Buzzard and eight of the Black Sparrowhawk. The perched birds are separately posed, leading to a better appreciation of each individual, and they are portrayed against a non-glare blue-gray background. Most of the 16 plates of perched raptors show eight or ten figures of four or five species on each. The eight plates of flying raptors are easily the best I have seen. The artist has shown soaring or flying eagles from below against a blue sky, while harriers and some hawks are shown from the side. The flying harriers and Chanting Goshawks are a stunning picture. Flying eagles and buzzards are good, but with some the tails are just not right, seemingly detached from the proper contour. But these plates by Arnot are really first rate and one wishes some of them were available as wall prints. Plate 16 would be a great day at Hawk Mountain, while the six owls of plate 23 are a work of art. Few artists can do a real eye-to-eye front view of a raptor, but the facing Bateleur on plate 2 is just right, and I wish it were a full plate. With over 280 figures of 80 species, it is no surprise that some are not correct in some details, but these are a remarkable set of raptor paintings, and I think incomparably better than those in Volume I of *Birds of Africa.* Most of the species are also shown in the 235 or so photographs, and 45 species have series of nest-side photos showing habitat, nest, eggs and stages of the young.

The text format includes English and Afrikaans names, scientific name and its derivation, identification (adult and immature), habitat, status and distribution, and general habits including much information on life history, nesting, food habits, etc. There are no measurements or technical descriptions but the identification includes diagnostic aspects of appearance, leg and eye-color, changes with physiologic state (e.g., in the Bateleur), as well as the feathering of both adults and immatures, particularly those aspects that may be seen in the field. The text coverage is interesting, often extensive, and it includes many recent findings.

The general reference list is followed by specific bibliographies for each of the 80 species, and the more important references each give a figure for the number of works listed, leading to a rapid "snow-balling" of literature. For the Black Eagle, for example, 31 papers are listed, of which that by V. Gargett lists 80 more references. This bibliography is very useful, enabling one to build up an excellent file in short order. No text citations are made, however, so one must guess about the source of new information on sexual dichromatism in the White-headed Vulture until one digs into the literature.

The African continent faces seemingly insurmountable overpopulation problems with disastrous consequences for both mammals and birds as habitats disappear in the ever-spreading demand for more food for ever more humans. The effects on raptors are often complex, as shown in Steyn's accounts of the Cape Vulture (which needs hyenas) and the Bateleur. The big-game parks are now the principal habitat of many raptors, and perhaps South Africa's parks may be more stable than those in East Africa. The Bateleur is still "common" in the Kruger, and long may it fly!

A number of impressive raptors, still inhabit southern Africa, some still frequent and others rare. It is good to have such readable up-to-date accounts of the Lammergeyer, Bateleur, Gymnogene, Bat Hawk, Secretary Bird, Palm-nut Vulture and the great eagles, although these last are better portrayed in Steyn's earlier *Eagle Days.* In writing this book, Peter Steyn says that he has written the kind of book he would like to have had when he started out to study raptors several decades ago. I think raptorphiles will agree he has accomplished his mission and with distinction. Color plates, photographs, line sketches, and range maps.—Walter R. Spofford.