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AN EVALUATION AND COMPARISON OF TECHNIQUES FOR ESTIMATING HOME RANGE AND TERRITORY SIZE

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ABSTRACT.—Estimates of territory and home range size can yield widely varying results depending upon methods of data collection and analysis. To evaluate the merits of different methods we examine space-use patterns of Pectoral Sandpipers (*Calidris melanotos*) and Red Phalaropes (*Phalaropus fulicarius*) on their breeding ground. We use empirical data from these species to generate a series of computer-simulated home ranges. We then examine the efficiency of a non-probabilistic estimator of territory size (minimum convex polygon method) vs two probabilistic techniques, one parametric (Jennrich and Turner 1969) and one nonparametric (Ford and Krumme 1979), testing for their sensitivities to sample size and to temporal dependence between successive observations.

All methods are sensitive to temporal dependence and sample size, but the probabilistic techniques provide better estimates from small samples. Both the minimum convex polygon method and the parametric Jennrich-Turner technique overestimate area utilized by the species studied here, both of which deviated from a bivariate normal distribution. The Ford-Krumme approach provided the most accurate estimate of utilized area.

The size of areas utilized or defended by individual birds frequently is an important datum sought in avian ecology. In this paper we explore problems associated with territory and home range size estimation, with an emphasis on statistical estimates of utilized rather than defended areas. We will use data from two species of shorebirds, Pectoral Sandpipers and Red Phalaropes. These species exemplify opposite extremes in territoriality: Pectoral Sandpipers achieve virtual exclusive use of their defended areas (Pitelka 1959), whereas, Red Phalaropes breed non-territorially (Kistchinski 1975). We will consider the efficiency of different estimators of utilized area as affected by sample size, temporal dependence between observations, and by differences in spacing behavior.

METHODS

ESTIMATORS OF UTILIZED AREA

Three general approaches are used in estimating utilized area. The oldest and most widely used is to draw a polygon connecting those observations that appear to lie on the periphery and define the area bounded by connecting these points as the size of the home range, territory, or utilized area. Observations may be defined as peripheral because they lie adjacent to regions never utilized (Stefanski 1967), because they lie on a boundary which the bird will not transgress when flushed (Wiens 1969), or because they form part of the convex hull of all observation points, i.e., the smallest set of points that when connected contains all other points (Weeden 1967). For this analysis we employ the last definition because it is mathematically definable. Its most important aspect relative to other definitions (below) is that it lacks a probabilistic description of their use of space ("space-use") within the bounded area.

Jennrich and Turner (1969) fit a bivariate normal distribution to the array of location points obtained by passive observation and then calculate the area of a 95% probability ellipse. An alternative, nonparametric, probabilistic estimator is described by Ford and Krumme (1979). This method utilizes the distribution of frequency of distances generated by taking all observation points pairwise. Ford and Krumme use a computer optimization algorithm to generate a simulated space-use distribution with a discrete distribution of frequency of distances as similar as possible to the observed data. The simulated space-use pattern is then integrated to estimate the minimum area that will contain a specified proportion, usually 95%, of the animal's space-use. This index, called MAP (0.95), may be calculated from simulated or observed space-use distributions. The method provides both a nonparametric probabilistic area estimate and also gives a visualization of the shape of the distribution.

DATA COLLECTION

Breeding male Pectoral Sandpipers and breeding female Red Phalaropes were observed at Barrow, Alaska, during June 1976 and 1978, respectively. Opposite sexes were used because the Pectoral Sandpiper is polygynous (Pitelka et al. 1974) while the Red Phalarope is polyandrous (Schamel and Tracey 1977). Study areas were marked off in 50 m grids and the locations of individuals were recorded to a 10 m resolution at 1 min intervals for study sessions running 50 to 200 min per session. Each individual was tracked for multiple sessions. For this paper we use data from three Red Phalaropes and three Pectoral Sandpipers. For analysis, observations were lumped into 50 × 50-m units. Cell areas referred to in the text are multiples of these 50 × 50-m (0.25 ha) grid units.

MOVEMENT SIMULATOR MODEL

Although the analyses we present are based on sequential sighting data for real birds, we have not used the raw data themselves directly, instead using them to construct a stochastic model designed to mimic the movement and space-use patterns of individual birds. After verifying that the simulator accurately mimicked the data, we then generated a series of simulated data sets.

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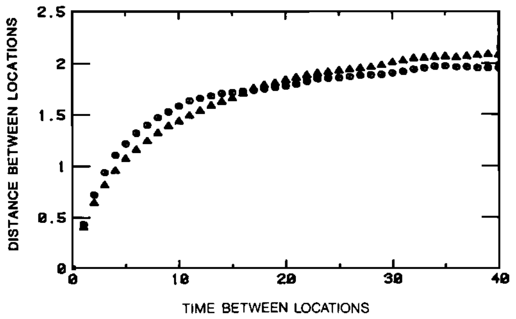

FIGURE 1. Average distances between observed locations as a function of the time separating observations. Time steps are 1 min, distance is in units of 10 m. Triangles are based on actual input data; circles are based on simulated movement sequences.

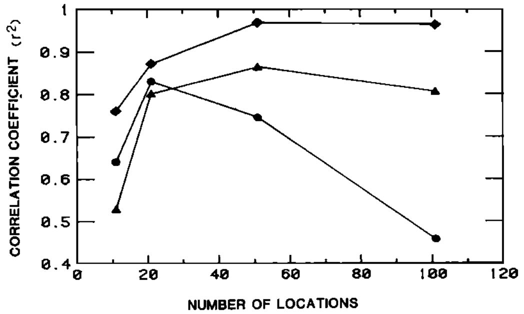

FIGURE 2. The correlation coefficient (r^2) of the regression of estimated individual utilized area size on actual 95% individual utilized area size as a function of sample size. Circles refer to polygon method, triangles to Jennrich-Turner index, diamonds to Ford-Krumme technique.

Two aspects of the movement patterns were considered to be important: the spatial distribution of sightings, and the relative frequency of distances moved between sightings. These distributions provide descriptions of two basic features of behavior that strongly influence the performance of space-use area estimators: (1) complicated nonuniform distributions; and (2) temporal dependence in movement pattern, usually with a series of relatively short movements interspersed with occasional longer movements. The result of (2) is that the expectation of distance moved between observations increases as the length of time between sightings increases.

The movement pattern is modelled as a Markov chain based on a $n \times n$ transition matrix where n is the number of grid cells contained in the territory. The transition probability from cell i to j is proportional to the joint probability of moving the distance D from the midpoint of i to the midpoint of j, $P(D)$, and the probability of moving to j, $P(j)$. We fit the model to a given individual by finding the sets of $P(D)$ and $P(j)$ which minimized the sum of squared differences between the observed and simulated frequencies of distances moved, and the observed and simulated frequencies of time spent in each cell. The minimization is carried out using a successive approximation computer algorithm.

TABLE 1

COMPARING THE ACCURACY OF UTILIZED AREA ESTIMATORS[a]

Estimate	Percent of true value ± 1 SD
Minimum convex polygon	
Pectoral Sandpiper	91 ± 12
Red Phalarope	200 ± 115
Jennrich-Turner	
Pectoral Sandpiper	129 ± 14
Red Phalarope	188 ± 26
Ford-Krumme	
Pectoral Sandpiper	101 ± 13
Red Phalarope	116 ± 23

[a] Values calculated from nine simulations per species, 251 locations per simulation, no temporal contingency between observations. Percent of true value was calculated for each simulation and averaged to obtain mean values ± 1 SD. Area is in grid units (0.25 ha).

The algorithm was successful at finding transition matrices that generated close fits of both movement rates and space-use for both species. Its success is shown by comparing the observed and simulated values for the average distance moved between locations as a function of the number of time steps between locations (Fig. 1).

TESTING THE ACCURACY OF AREA ESTIMATORS

Three sources of error can bias estimates of utilized area: sample size; temporal contingency between successive observations; and deviations from an assumed underlying distribution, such as bivariate normality. We examined the effects of these biases using output from the movement-mimic model described above. For each of the six individual real data sets, three from each species, we generated simulated observations involving 1000 locations per record. Each set was replicated three times, for a total of 18 simulated bird movement patterns. Three data sets were generated separately for examining the effect of temporal contingency: successive observations separated by 1 time step, 10 time steps, or completely independent in time. Curves of estimated utilized area versus number of observations were then generated for each data set using the different area estimators. We compared these estimates with the true MAP (0.95) values calculated directly from the simulated records.

RESULTS

Mean utilized area (MAP 0.95) for simulated Pectoral Sandpipers and Red Phalaropes were 18.4 and 14.6 grid units, respectively. These true values, calculated directly from the model output, are compared with estimates of the different indices in Table 1. For both species the Ford-

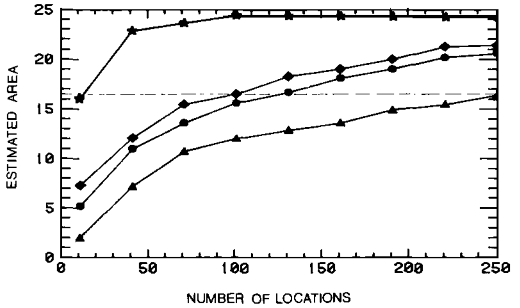

FIGURE 3. Estimated average utilized area in grid units (0.25 ha) as a function of sample size using the minimum convex polygon method. Triangles represent observation sequences with 1-min intervals, circles with 10-min intervals, and diamonds sequences where successive locations are independent. Stars represent the territorial flushing model described in text. Dashed line represent true values calculated directly from simulated data sets (MAP 0.95, see text).

Krumme method gave the closest estimates to true values.

As an alternative to providing absolute estimates of utilized area, these indices may also be used to compare populations or individuals. Such a relative test requires only that the index be highly correlated with true size. To compare the estimators in this regard we correlated average index values with their corresponding true MAP (0.95) values for data sets with complete independence between observations.

Both probabilistic estimators become more accurate with increasing sample size (Fig. 2), and the nonparametric index is consistently more accurate than the parametric technique. The polygon method, by comparison, becomes less effective with increasing sample size. The downward trend in r^2 occurs as the index is progressively dominated by low probability regions in the periphery of the utilized area.

For samples without temporal contingency, the polygon method generates estimates that increase monotonically with increasing numbers of location records, but only slowly does it approach a limit (Fig. 3). The greater the contingency between successive observations, the slower the approach.

The very large number of observations required by the polygon method may be reduced significantly if the observer actively flushes the bird to its territorial boundary (Wiens 1969). This situation was modelled by generating distributions based on the same data set, but modified so that only grid cells bounded on at least one side by non-utilized area were included in the distribution. Assuming a "best case" of no contingency between observations and all perimeter cells equally likely, this method approaches an asymptote in fewer than 100 observations (Fig. 3).

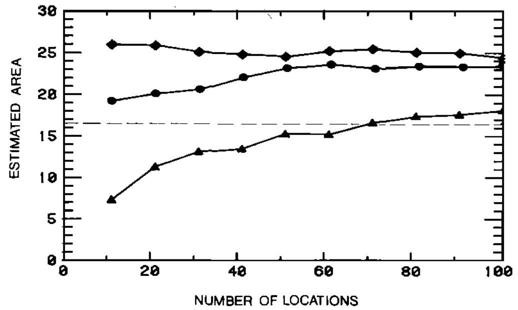

FIGURE 4. Same as Figure 3 but for the Jennrich-Turner index.

The Jennrich-Turner method requires a much smaller sample size to achieve stability (Fig. 4). Stable estimates may be obtained with 10 or fewer observations per individual if successive observations are independent. With moderate temporal contingency, however, the index may require as many as 50 to 100 observations, and even more with high contingency.

The nonparametric method (Ford and Krumme 1979) performs similarly to the Jennrich-Turner method in its sensitivity to sample size, but it is somewhat more affected by temporal contingency (Fig. 5). At maximum contingency the index is strongly affected and the area estimates remain low even after 500 observations. For independent observations, however, the index is very stable, and as noted above it provides a better estimate of true value (Table 1; compare Figs. 4 and 5).

DISCUSSION

The polygon method is a poor choice for estimating utilized area despite its widespread use (Table 2). This index is strongly affected by sample size and requires prohibitively large sample sizes to reach an asymptote. The rate of approach to the asymptote is so slow even with little temporal dependence among observations that it is unlikely that many fieldworkers would be able to obtain the required data set. Further, there is virtually no way to determine what proportion of the asymptotic limit has been reached at a given sample size. Finally, the actual area estimated is much larger than true value. Thus this method presents serious interpretive problems, difficulties not offset by its seductive simplicity.

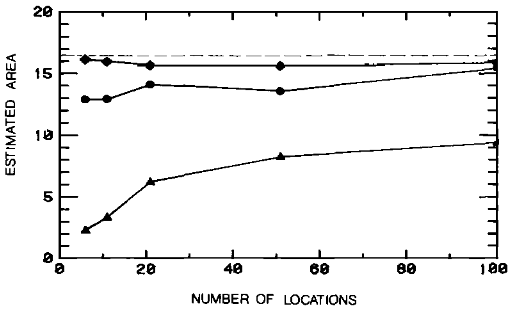

FIGURE 5. Same as Figure 3 but for the Ford-Krumme index.

The Jennrich-Turner method provides a stable area estimate based on a relatively small number of independent observations, and it appears to be the least sensitive method to temporal contingency. Its assumption of bivariate normality, however, creates problems. For the data analyzed here, the 95% use area estimated by the Jennrich-Turner technique is almost half again as great as the true value (Fig. 4). Such a bias may not occur if the distributions are more nearly normal. Although Zack and Falls (1978) found that song territories of male Ovenbirds (*Seirus aurocapillus*) are approximately bivariately normal, this assumption probably is not met widely. It is certainly violated by the data sets used in this study, as well as by space-use distributions of Buff-breasted Sandpipers (*Tryngites subruficollis*) (Ford and Krumme 1979) and Sanderlings (*Calidris alba*) (J. P. Myers, unpubl. data) on their wintering grounds. As a relative size index, the Jennrich–Turner method performs well even for non-normal distributions.

The Ford-Krumme method is superior to the Jennrich-Turner approach when normality is violated. It provides accurate estimates of absolute area even with small sample sizes, provided that successive observations are independent. It is also an effective tool for examining relative differences, showing consistently higher correlations with actual individual area values than do either alternative. Its principal disadvantage is its relative expense in terms of computer time.

CONCLUSIONS

For absolute estimates and relative comparisons of utilized areas, the probabilistic techniques of Jennrich and Turner (1969) and Ford and Krumme (1979) clearly surpass the minimum convex polygon technique. If the underlying distribution is already known to be bivariately normal, then the Jennrich-Turner parametric method offers an efficient estimator of utilized area. If, however, the underlying distribution is either not normal or is unknown, then the Ford-Krumme approach should be taken.

Our comparisons illustrate a clear basis for selecting the probabilistic nonparametric estimator (Table 2). But what if the parameter of interest is defended area, instead of utilized? For species where these are synonymous, results should be the same. But when defended area deviates from utilized area (Stefanski 1967, Zach and Falls 1979, Tryon and MacLean 1980), then the method of choice may change as a function of statistical factors we have yet to examine. Ultimately, then, as with so many other measurements made in avian ecology, the choice of technique depends not only on statistical considerations but also on a clear perception by the investigator of the questions under study, and

TABLE 2
RELATIVE ADVANTAGES OF DIFFERENT ESTIMATORS OF UTILIZED AREA

Estimator	Advantages	Disadvantages
Minimum convex polygon		
Passive observation	????	—requires enormous samples —highly sensitive to contingency —uninterpretable estimate
Territorial flushing	—simple, cheap	—overestimates utilized area
Jennrich-Turner	—calculation relatively simple, inexpensive —good predictor if bivariate normal —efficient with modest sample	—assumes bivariate normality —sensitive to contingency
Ford-Krumme	—assumes no distribution —excellent predictor even with small sample	—sensitive to contingency —expensive, requires computer

a sound appreciation of the system's biological details.

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