MEASUREMENT OF TERRITORY AND HOME RANGE SIZE IN BIRDS

BY EUGENE P. ODUM AND EDWARD J. KUENZLER

AT some time during the annual cycle, most vertebrates restrict their activities to a definite area which may be termed the home range. If all or part of the home range is defended against other individuals of the same species, the guarded area is called a territory, according to current usage. Territoriality is an important mechanism which reduces intraspecific competition; it is especially pronounced in nest-building animals (birds, certain fish, insects, etc.) which have complicated behavior patterns requiring highly coördinated actions during reproductive periods. Establishment of territories and home ranges produces characteristic intrapopulation distribution patterns which have important bearing on the choice of census methods (See Odum, 1953, Chap. 6).

Examination of the voluminous literature on territorialism in birds reveals that many qualitative details have been worked out. The "kinds" of territory, such as are listed in the comprehensive review by Nice (1941), have been classified, and the means of establishment and defense of the territory area have been described for many species. On the other hand, many quantitative aspects of territorialism have been scarcely considered. For example, the effect of various populations and habitat factors on the size and configuration of the defended or occupied areas is virtually unknown. A relation between territory size and food supply is often postulated, but we know of no case where the available food supply and the size of territory have both been accurately measured. It is true that numerous estimates made of territory size have been published, but it is evident that many are but crude approximations, often based on less than a dozen spot observations. Very little confidence can be placed in the comparison of measurements made by different investigators because of the great variation in procedures used and in the intensiveness of the observation. It is becoming quite evident that quantitative comparisons of territoriality cannot proceed until sound, consistent methods of measurement are developed.

In this paper the problem of measurements of territory and home range size is critically examined, and a method for standardizing measurements is proposed. The method is illustrated by data obtained in a study of territoriality of seven southeastern species. These data are also used to test certain concepts developed by mammalogists in their parallel studies of home range.

The present study is part of an ecological survey being conducted on the Savannah River Area by the University of Georgia under contract No. AT (07–2)–10 with the United States Atomic Energy Commission. These investigations are designed to establish present population levels and trends of major terrestrial organisms in order to facilitate future analysis of changes resulting from the complete removal of the resident human population and the operation of atomic energy installations, as well as to provide a basis for land management. The Savannah River Area comprises about 200,000 acres on the upper coastal plain in Aiken and Barnwell counties, South Carolina. Since the most feasible method for measuring the density of breeding birds on large areas is the "territory-mapping" method, it was necessary that we obtain data on territory size of important species of the region.

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The Concept of Maximum Territory and Utilized Territory.—The method generally used to determine the size of the territory (defended area) or home range (in case the area is not defended) in birds has been to plot the location of the male or the pair at different times directly on a map carried into the field. The outermost points on the map are then connected forming a polygon, the area of which may be determined. If the territory is irregular in shape, as is often the case, differences in area would result depending on how the points are connected to form a polygon. If the extreme outermost points are connected with straight lines so as to include all the other points, a larger area results than if the line is drawn connecting all of the perimeter points. In the former case there is only one polygon possible, while in the latter case one would have to decide, often without observational data, which points were actually the outside boundary or perimeter points. Consequently, it seems best first to measure the *maximum territory* by connecting the extreme points with straight lines as indicated above, and second, to determine by other means what proportion or percentage of this maximum territory is the *utilized territory.* The utilized territory, of course, will depend on the distribution of habitat features within the maximum territory area, the location of singing perches, feeding and nesting sites, and whether the male or pair actually makes use of all the defended area. The concept of maximum and utilized territory is analogous to the recognized concept of crude and specific (or ecological) density. For example, we might have 20 birds of a particular species on 100 acres of land; the crude density would be 20 per 100 acres. If, however, there were only 50 acres of habitat suitable for the species within the 100-acre tract, then the specific density would be 40 per 100 acres. Likewise, a male or pair might defend or visit points around an area of 10 acres, but actually utilize only half of the area or 5 acres. A similar comparison might be made between crude birth rate and specific birth rate. It is evident that the maximum territory (as well as crude density or birth rates) will be easier to determine than the utilized territory (or specific density and birth rate) yet the latter may often have more biological meaning.

The present paper is concerned with two methods of measuring and expressing the maximum territory or home range, leaving the problem of estimating the utilized territory or home range for further study.

The Observation-Area Curve.—Three tracts on the Savannah River Area were selected for intensive study. The first contained mature deciduous woods, pine woods, abandoned fields, and a lake margin. The second site contained an abandoned house site surrounded by abandoned fields and hedgerows. The third study area was a "Carolina Bay," a shallow depression of unknown geological origin covered, in this case, with grassland vegetation. Large maps of each of the tracts were prepared by use of plane table or compass and jake-staff, with distances measured by surveyor's chains and by pacing. Aerial maps were also available. From the base maps sketch maps of portions of the study tracts were made for use in the field as needed.

The commonest breeding species—for example the Kingbird (*Tyrannus tyrannus*), Wood Pewee (*Contopus virens*), Meadowlark (*Sturnella magna*), and Orchard Oriole (*Icterus spurius*)—were studied. When a pair was located, often by first locating the nest, the birds were observed continuously for periods of one-half hour to three hours in the mornings and late afternoons, and the location and activities of individuals at approximately five-minute intervals were plotted on a field map made from the reference base map. The male was given primary attention, but wherever feasible the location of the female was also plotted. All major changes in location were plotted even though they did not occur exactly at the five-minute check times, but observations were standardized so as to yield an average of 12 spot locations per hour. The points were treated as "recaptures" somewhat comparable to those made using live-traps in population studies of mammals. Data on a total of 37 pairs representing 9 species were available for the following analysis.

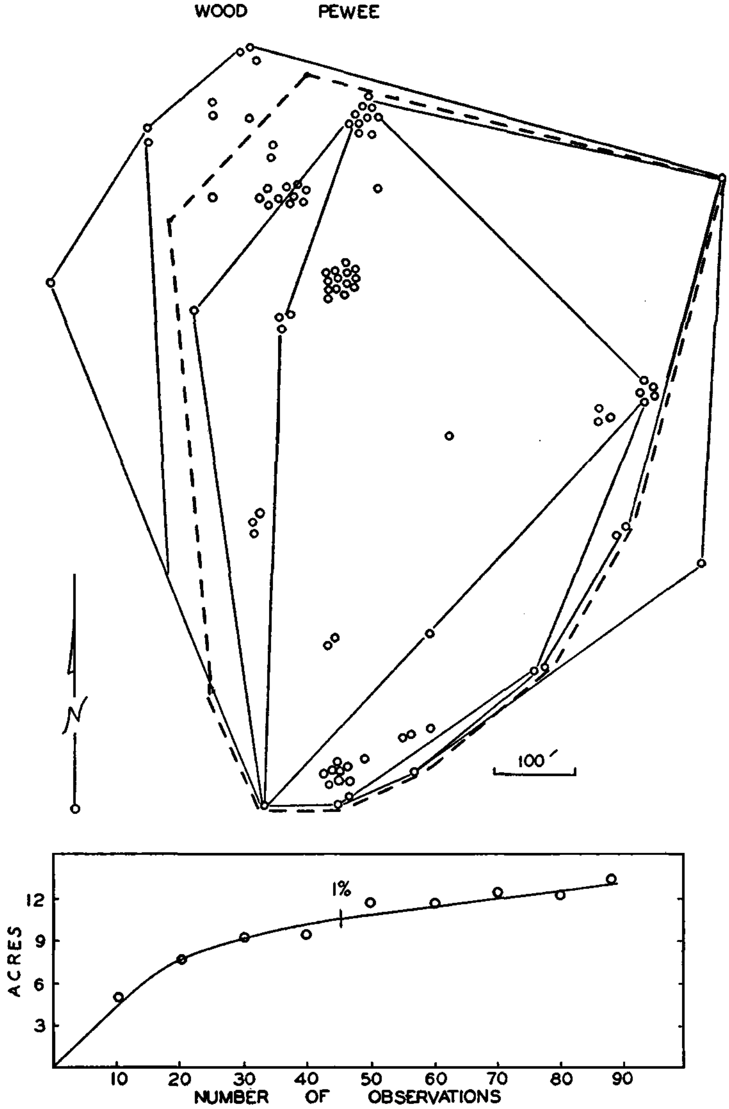

FIGURE 1. Observed positions of a male Wood Pewee at five-minute intervals (small circles) with maximum observed area enclosed in solid lines after successive tens of observations. The broken line in the upper diagram encloses the calculated maximum territory size (10.8 acres) at the one per cent level as shown on the observation-area curve below.

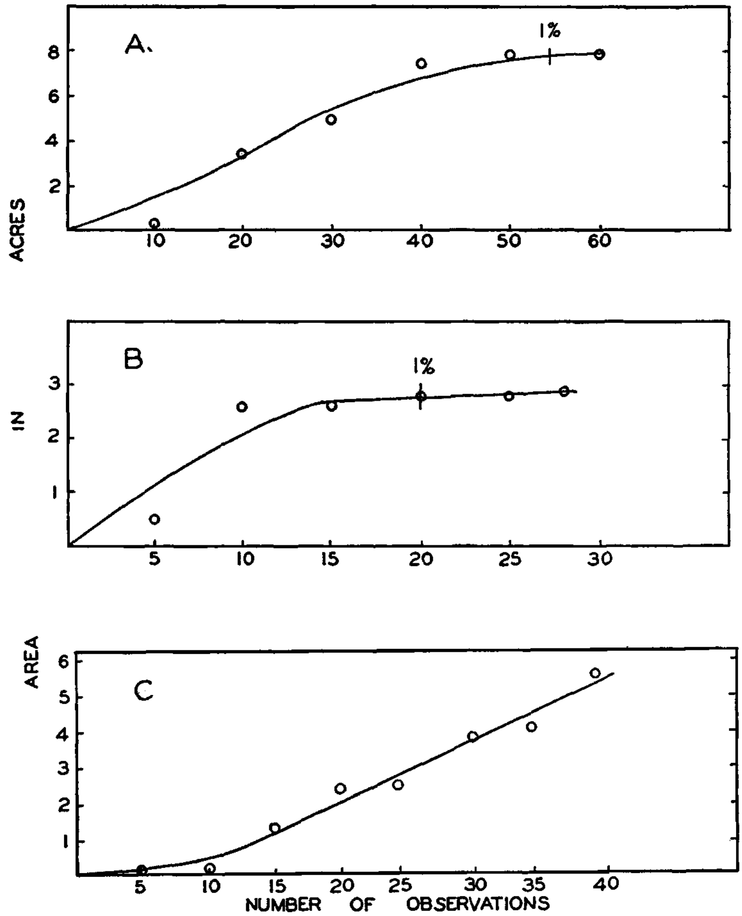

FIGURE 2. Observation-area curves for: A, Chipping Sparrow during nest building and incubation stages; B, same pair of Chipping Sparrows during nestling stage (see table 1); C, Blue Grosbeak during nest building and incubation stages.

To compute the maximum territory, an "observation-area" curve was used, adapted from the "species-area" curve used by ecologists for the determination of the minimum sample area that contains an adequate representation of the species present in a plant community (see Cain, 1938). After each series of 10 consecutive observations, the outermost points were connected as shown in figure 1 and the area of the polygon measured with a planimeter. As the number of observations increased, the size of the area increased as shown in figure 1 with a point being reached where continued observation resulted in little or no observed increase. If the same relative point on each curve is selected, then a comparable measure of territory size is thereby obtained. A one percent level, that is, a point on the smoothed curve beyond which each additional observation will produce less than one percent increase in the area (or each 10 observations less than 10 percent increase), appears to be a good, practical point to use. Although this is an arbitrary end-point, it represents a point of diminishing returns, it is independent of the total number of observations or the size of the territory, and it is comparable regardless of the species or stage in breeding cycle being considered.

Three other observation-area curves are shown in figure 2. In one of these not enough observations were made to reach the leveling-off point, and therefore, territory size could not be determined in this case. In using this method one would need to plot the areas after each period in the field in order to determine whether enough observations had been made to locate the one percent change level; if not, it would be necessary to continue the field observations. Where the occupied area is large or the behavior of the bird erratic, a longer time will be required. For the species so far studied it was found that from 25 to 90 spot observations, or 2 to 8 hours of field observation, were required to reach the one percent level. Thus, in most cases, two or three hours of observation in the mornings of two or three days sufficed for measurement of the size of the area occupied during that period. This rapid determination makes it possible to study changes in territory size that may occur during successive changes in the nesting cycle, i.e., nest building, incubation, nestling, and fledgling periods.

It should be pointed out that the observation-area curve merely aids in standardizing determinations of the size of an occupied area. Whether this occupied area is to be classed as a territory or a home range depends on the observed behavior of the occupants. Thus, the Kingbird is strongly territorial and defends all of its occupied area. On the other hand, we observed that several pairs of Orchard Orioles often nested close together and shared a common feeding ground. Most of their occupied area would thus be classed as a home range.

Two examples will serve to illustrate how the observation-area curve may be used in the study of fundamental quantitative aspects of territoriality. In table 1 territory size at successive stages in the nesting cycle is compared. In each case, the size of the occupied area was calculated by means of the observation-area curve while the pair was engaged in nest building and incubation. Then, the entire procedure was repeated when the pair was engaged in feeding the nestlings. Since there was no evidence of separate territories

TABLE 1

TERRITORY SIZE AT THE ONE PERCENT LEVEL AT SUCCESSIVE STAGES OF THE NESTING CYCLE

	Nest building and incubation stage	*Nestling stage*
Kingbird pair No. 1	14.0 acres	9.3 acres
Chipping Sparrow pair No. 1	7.6 acres	2.7 acres
Blue Grosbeak pair No. 1	15.3 acres	13.0 acres

for male and female in these cases, the areas tabulated include that occupied by both members of the pair. In all three species the territory size was much less while the adults were engaged in feeding nestlings than when the pair was engaged in nest building and incubation. If this proves to be a general rule, it would provide strong evidence against the theory that territoriality functions primarily in preserving a food supply, since the area used is smallest when need for food is greatest.

Table 2 illustrates something of the individual variation found in territory size of two species when engaged in the same phase of the nesting cycle, namely, nest building and incubation. The Kingbird exhibits type "A" territory, i.e., the male defends the mating, nesting, and feeding ground (see Nice, 1941), whereas in the Redwing (*Agelaius phoeniceus*), the male defends only the nesting area (type "B" territory).

TABLE 2

VARIATION IN TERRITORY SIZE IN DIFFERENT INDIVIDUALS ENGAGED IN SAME STAGE OF THE NESTING CYCLE (NEST BUILDING AND INCUBATION)

	Pair number	*Acres*
Kingbird	1	14.0
	3	35.0
	4	17.5*
	8	16.4
	Male number	
Red-wing	2	1.6
	4	1.1
	5	4.2

* Narrow territory

Territory or Home Range Expressed in Terms of an Activity Radius.—Dice and Clark (1953) have pointed out that in many species of mammals the individual has no fixed limits to its wanderings, and therefore, an attempt to ascertain home range boundaries or to express home range in terms of area is unsatisfactory. They suggest that home range in such cases is better expressed in terms of an "activity radius," and the authors utilize data obtained in a live-trapping study of the white-footed mouse (*Peromyscus maniculatus bairdi*) to illustrate certain possibilities of this procedure. For each marked animal captured more than once a geometric activity center was determined and the distance from this center to each recapture point designated as a recapture radius. When the square roots of 119 recapture radii (representing a number of individuals) were plotted

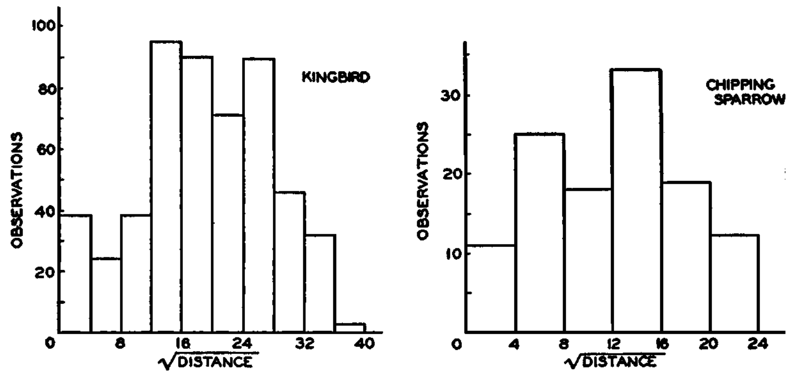

FIGURE 3. Frequency histograms of square roots of 524 activity radii for Kingbirds and 118 activity radii for Chipping Sparrows. For the Kingbird, β_1 (a measure of skewness) is 0.0351 (not significantly different from zero), and β_2 (a measure of kurtosis) is 2.238 (significantly different from 3 or normal). For the Chipping Sparrow, β_1 is 0.0057 (not significantly different from zero), and β_2 is 2.032 (significantly different from 3). Thus, both histograms are normal but exhibit platykurtosis.

as a frequency histogram, the resulting curve was essentially normal, exhibiting positive skewness but no kurtosis. Thus, a mean activity radius subject to standard statistical treatments could be calculated. Dice and Clark suggested that if animals defend territories (not the case in *Peromyscus*) their movements would tend to be restricted, which should, theoretically, result in "a certain amount of kurtosis in the frequency curves for the recapture radii."

To test these concepts the same procedures as used by Dice and Clark were applied to our bird data. For each of five pairs of Kingbirds and two pairs of Chipping Sparrows (*Spizella passerina*), a geometric activity center was determined and activity radii measured. Using a square root transformation, the frequency distribution of 524 activity radii for the Kingbird and 118 radii for the Chipping Sparrow is shown in figure 3, together with the calculated values of B_1—a measure of skewness, and B_2—a measure of kurtosis. Both frequency curves are essentially normal without skewness (B_1 not significantly different from 0) but both exhibit platykurtosis (B_2 significantly less than 3 at the 5 percent level). Thus, the prediction of Dice and Clark is borne out by our data. It would seem that testing for platykurtosis in frequency distribution of activity radii is a good method of determining whether an animal's occupied area has a definite boundary as a result of territorial defense or other reasons. We also interpreted these results to mean that territorial birds do have relatively fixed limits (as compared with *Peromyscus*) at least during a given phase of the breeding cycle. Therefore, the territory may be expressed in terms of area rather than merely as an activity radius, and the use of the observation-area curve to determine the area is justified.

Summary.—It is suggested that the distinction between *maximum* territory (defended area) or home range (in case area is not defended) and *utilized* territory or home range simplifies the problem of quantitative measurement.

When observed size of the occupied area was plotted against the number of observations made at 5-minute intervals, characteristic "observation-area" curves were obtained (figures 1 and 2), which can be used to standardize measurement of size. The one percent level on the smoothed curve is suggested as a suitable point to use in comparisons; it is arbitrary but represents a point of diminishing returns, is independent of the total number of observations or the size of the territory, and is comparable regardless of species or stage of the breeding cycle.

The use of the observation-area curve is illustrated by a comparison of territory size at successive stages in the nesting cycle of the same pair (table 1) and at the same nesting stage in different individuals (table 2).

An alternate procedure, that of expressing territory size in terms of an activity radius, is tested employing the method used by Dice and Clark in a study of home range in deermice. The frequency polygons for Chipping Sparrows and Kingbirds were essentially normal but exhibited platykurtosis which is interpreted to mean that territorial birds, in contrast to mice, are relatively fixed in their movements during a given phase of the nesting cycle. Therefore, the expression of territory size in terms of area and the use of the observation-area curve are justified.

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