

# Mechanisms and Evolution of Spacing in Animals

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Animals of the same species are rarely distributed randomly. Each individual's movements are influenced by those of its neighbors, with the result that any population exhibits a characteristic pattern of individuals' locations and activities in space.<sup>1</sup> In this chapter, we discuss in turn three approaches to understanding individuals' spatial relationships: quantitative specification of patterns of spacing; analysis of the behavioral mechanisms that control spacing; and identification of the effects of natural selection on the evolution of spacing. This division separates discussion of the proximate controls of spacing, in our initial sections, from consideration of the ultimate controls, with which we conclude.

The literature on spacing relies heavily on two simple concepts: home range and territoriality. Recently, it has become apparent that important variation in spacing patterns and mechanisms is concealed by the application of these common terms. Consider "territorial" birds. In some species, like bicolor antbirds (*Gymnophithys bicolor*) (Willis, 1967), individuals overlap widely in their movements, although each manifests clear dominance over intruders within its territory. In other species with similar patterns of spatial variation in dominance, individuals

<sup>1</sup>Where individuals form cohesive groups, these groups often behave in a manner similar to that of individuals in more solitary species. Except in discussions of fitness or unless otherwise indicated, the term *individual* in this paper includes cohesive social groups.

occupy largely exclusive areas. Tree sparrows (*Spizella arborea*) provide a well-documented example (Weeden, 1965). Tree sparrows and antbirds thus share "territorial" characteristics in spacing behavior, but they differ dramatically in the degree of isolation they maintain from neighbors. It is time to recognize that spatial variation in an individual's agonistic behavior, activities, and isolation from neighbors varies in complex ways from species to species.

In this chapter, rather than pursue unitary concepts, we attempt to address this variation in spacing by examining methods for measuring spatial patterns of individuals' activities, isolation, and aggression; by considering the behavioral mechanisms that can control these manifestations; and by proposing a framework for explaining their evolution.

In the first section, "Quantitative Description of Spacing Patterns," we review attempts to measure aspects of spacing. For clarity in describing variation in spacing patterns, we introduce the use of two "fields" (Wiley, 1973; Black and Wiley, 1977), which can be defined for any individual.

The distribution of an individual's time as a function of location defines an *activity field*. The word *field* is used here in the mathematical sense as "a function of . . . position in space measured in a rectangular coordinate system" (Feynman, Leighton, and Sands, 1964, II:2-2). The value of an individual's activity field at any point is the proportion of its time spent there in all activities. The boundaries of this field delimit the individual's home range or activity space (Burt, 1943; Weeden, 1965). Alternatively, such a field could include only particular activities of importance to resource use, for instance, time spent feeding. An activity field that pertains to an individual's use of a particular resource is sometimes called a "utilization distribution" (van Winkle, 1975).

The relative exclusiveness of an individual's use of space as a function of location further defines an *isolation field*. The value of an individual's isolation field at any location  $(x, y)$  is the ratio: time spent by the subject at location  $(x, y)$  divided by time spent by all individuals including the subject at  $(x, y)$ . This ratio varies from 1, when the subject has exclusive use of the location, to 0, when the subject never uses the location but others do. A set of individuals' isolation fields thus both describe their pattern of spacing and, in combination with information on resource distribution, indicate the degree to which each individual monopolizes access to resources.

In the second section, "Behavioral Mechanisms of Spacing," we discuss the behavioral tendencies that are the proximate determinants of spacing patterns. As Marler (1976) has emphasized, the same spacing pattern can in principle arise through alternate behavioral strategies of individuals. Consider arboreal forest primates that maintain largely exclusive territories: in some, like titi monkeys (*Callicebus moloch*) (Mason, 1968; Robinson, in press), gibbons (*Hylobates lar*) (Ellefsen, 1968), and red-tailed monkeys (*Cercopithecus ascanius*) (Struhsaker, 1975), close-range aggressive encounters at boundaries are a regular feature of neighboring groups' interactions; in others, like blue monkeys (*Cercopithecus mitis*) (Struhsaker, 1975), black-and-white colobus (*Colobus guereza*) (Marler, 1972; Struhsaker, 1975), and some howler monkeys (*Alouatta* species) (Chivers, 1969; Altmann, 1959; Neville, 1972), neighboring groups meet at close range much less

frequently. In the latter species, loud calls seem to aid in maintaining distance between neighboring groups without frequent close-range encounters, while in titi monkeys and gibbons, loud calls at dawn seem, in contrast, to lead neighboring groups into close-range interactions at boundaries. Similar patterns of isolation are maintained by different balances between overt aggression and avoidance.

The behavioral "rules" that determine spacing in a population will, in general, be influenced by the previous histories of individuals, the identities and characteristics of opponents, the proximity of opponents, and especially the location of encounters. The last of these effects produces spatial variation in individuals' agonistic tendencies. Because this phenomenon has such crucial importance for spacing, we introduce a third field (Wiley, 1973), an *aggression field*; the value of an individual's aggression field at any location is defined by its probability there of attack or retreat. Determining the way in which aggression and activity fields interact to produce the pattern of isolation fields in a population is a basic goal for studies of spacing.

In the third section, "Communication of Advertisement and Threat," we take up the use of signals as substitutes for physical contact. Spacing signals greatly increase the area over which an individual influences its neighbors' movements; in this section, we discuss constraints on the evolution of such signals.

In the fourth section, "Evolution of Spacing Behavior," we turn to the evolution of the diversity in patterns of animal spacing. Most previous evolutionary explanations for spacing patterns have addressed the relative advantages and disadvantages of the defense of a resource. But defense is not a simple phenomenon, particularly when alternate behavioral mechanisms can lead to isolation. We develop theories that deduce the optimal spacing of resident individuals in a population from the spatial and temporal distribution of critical resources. This approach provides more comprehensive evolutionary explanations of relationships between movement patterns and isolation fields of individuals in a population.

## QUANTITATIVE DESCRIPTION OF SPACING PATTERNS

### ACTIVITY FIELDS AND MOVEMENT PATTERNS

The first challenge in a study of spacing is a choice of methods for recording and then measuring the movements of individuals and the consequent activity and isolation fields. The technique selected for recording animals' movements can constrain the range of answerable questions about spacing.

Methods for recording animal movements have ranged from direct observation of individuals (e.g., Altmann and Altmann, 1970; Gottfried and Franks, 1975; Struhsaker, 1975) to such imaginative indirect methods as positioning smoked kymograph paper in the pathways used by individually toe-clipped mice (Justice, 1961; Metzgar, 1973a) or mounting spools on the backs of turtles, which then leave their tracks in unwound thread (Stickel, 1950). Field methods usually

require some trade between the time or effort required and the quality of data obtained (see Sanderson, 1966; Taber and Cowan, 1971). In addition, methods differ in suitability for measuring the spatial distribution of an individual's time, as opposed to the temporal sequence of its movements.

Direct observation of an individual yields the greatest information: the overall area used by the individual, the distribution of the individual's time within that area, and the spatial distributions of particular behavior patterns. Direct observation also gives information on location as a function of time, including rates of movement and rates of return to specific areas. Complete information is, however, acquired at the cost of considerable time and effort and requires an easily observable subject. Tagging individuals with visual, radioactive, sonic, or radio beacons can facilitate direct visual observation (Montgomery, Cochran, and Sunquist, 1973; Buchler, 1976), but in practice, information must often be sacrificed through the use of tracking or mark-recapture techniques.

Tracking methods can often be devised for animals not observable by direct means. These techniques preserve information on sequence of movement, but they often lose information on variation in rates of movement and are of limited use in measuring the form of activity fields. As a result, tracking methods are most useful where the details of neighbors' movements relative to each other are of interest (Peters and Mech, 1976) or where they generate data on the distribution of behavior patterns, such as site-specific defecation, which are relevant to interindividual spacing (Bearder and Randall, 1978).

Mark and recapture methods retain information on the form of activity fields but lose all information on movements within the intervals between captures. "Capture" need not disrupt the movements of the animals under study; repeated censusing of banded birds, radio fixes, detection of radioactive tags, and use of dyes to generate marked urine or feces (Frantz, 1972; Evans and Griffith, 1973) are all forms of mark-recapture methods. Recording of individually distinctive tracks on kymograph paper, photography of birds and mammals by activity-triggered remote cameras, and microphone arrays to record locations of loud vocalizations (Schleidt, in press; Watkins, 1976) are similar to mark-recapture methods in recording the locations of individuals at irregular intervals. Although such techniques are often simpler than direct observation or tracking, they can have the disadvantage of recording locations only during certain activities. In particular, locations at which individuals are live-trapped can misrepresent the overall use of space by those individuals (Brown, 1962; Metzgar, 1973a; Robinson and Falls, 1965). "Over a period of time the investigator accumulates a series of dots on a map or chart and is not certain what they mean, and rarely knows why the animals came near the traps when they were caught" (Sanderson, 1966, p. 222).

Despite this shortcoming, for many species mark-recapture techniques are the only feasible way to record movements. If captures or observations are repeated at time intervals that are reasonably short in relation to the animal's rate of movement, mark-recapture becomes a form of instantaneous sampling (J. Altmann, 1974) and can in principle be used to estimate both activity-field and sequence-of-movement data. Statistical techniques for assessing the reliability of such estimates are not, as yet, available.

The next decision in a study of spacing is a selection of procedures for the quantitative description of an individual's use of space. The traditional measure of an animal's use of space is home range size. Home range, "the area over which an animal normally travels in pursuit of its routine activities" (Jewell, 1966, p. 103), has been widely accepted as an indication of the amount of space (and, by extension, resources) used by an individual (McNab, 1963; Schoener, 1968a; Turner, Jennrich, and Weintraub, 1969). Home range area, or more precisely the area enclosed by a convex perimeter around an animal's locations, is attractively simple as a measure of the spatial distribution of its activities. Nevertheless, the concept has serious drawbacks.

Much disagreement has resulted from conflicting conventions in estimating home range size (Sanderson, 1966). The application of a variety of commonly used techniques to the same set of data obtained by continuous following of individuals can yield measures of range size that differ severalfold (Waser and Floody, 1974). Problems become especially severe when an individual's activities are concentrated in a relatively few scattered locations and the intervening areas are occupied briefly in passing, if at all. For instance, in feral cats the area utilized "consists of a varying number of more or less regularly visited localities connected by an elaborate network of pathways" (Leyhausen, 1965, p. 252). This situation seems to characterize many mammals (Ewer, 1968; see Adams and Davis, 1967; Bailey, 1974; and Eaton, 1970, for recent examples) as well as other animals, like butterflies, bees, and hummingbirds, which practice "trap-line" foraging (Janzen, 1971). In these cases, the size of an animal's home range has no clear relation to its ecology or behavior.

A more general problem in estimating the sizes of home ranges arises from effects of the length of study. Cumulative range size tends to approach an asymptote as length of sampling time increases. To reduce the effects of sampling time, Odum and Kuenzler (1955) have suggested that range size be defined at the point where each further observation increases the measured area by 1% or less. Other methods for estimating the asymptotic area of a home range, analogous to those for estimates of species number from nested quadrats in botanical communities (Preston, 1962) or repertoire size from samples of the frequencies of behavior categories (Fagen and Goldman, 1977), have not, to our knowledge, been applied to home range data. Any estimate of the asymptotic area of a home range encounters problems when animals focus their activities successively in different subsections of their ranges. Then, the cumulative home-range area passes several successive "asymptotes," like steps, as observations continue (Figure 1).

Temporary shifts in habitat use, occasional movements outside the usual area, unutilized "lacunae," and other manifestations of uneven use of space make it virtually impossible to propose universally satisfactory methods for measurement of home range size. Yet, just such complications may have critical consequences for spacing. This dilemma points up the major shortcomings of any single parameter, like area, as a measure of the distribution of an animal's activities in space. Intensity of use varies with location; an activity field is rarely specified by one parameter.

Probabilistic models of home ranges provide a limited analysis of differences

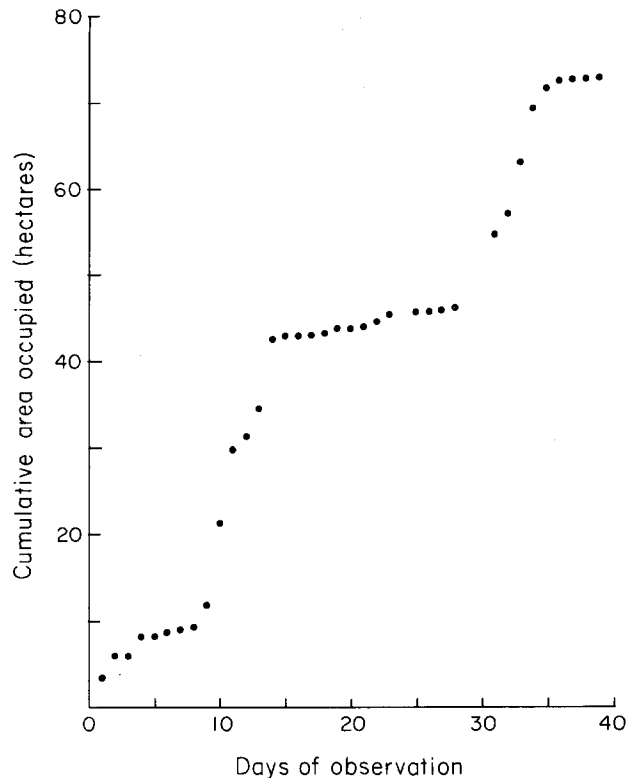


Fig. 1. Cumulative area occupied by one mangabey group. The group was followed continuously. From Waser and Floody, 1974.

in the intensity of an individual's use of locations. These models require stringent assumptions concerning the form of the activity field: probability of use must fall off from the center of the home range according to a specified probability distribution, either univariate (Dice and Clark, 1953; Hayne, 1949; Harrison, 1958; White, 1964) or bivariate (Calhoun and Casby, 1958; Jennrich and Turner, 1969; Metzgar, 1972; Mazurkiewicz, 1971). The use of two parameters to describe an activity field, in bivariate models, is potentially a modest advance over a single parameter, like asymptotic home-range size. These models require "that the actual utilization distribution conform to rather specific constraints . . . which are frequently not satisfied, even within rather homogeneous habitats" (van Winkle, 1975, p. 12). Worse, where spacing is at issue, the properties of the assumed probability distribution are most crucial at the edge of the home range, where data are often least adequate.

A more complete description results from the tabulation of intensity of use on a grid of quadrats superimposed over the home range. Continuous (or instantaneously sampled) data have been transformed into maps of intensity of use by molding and weighing clay "tracks" (Adams and Davis, 1967), by hand tabulation of observational data (Weeden, 1965; Chivers, Raemakers, and Aldrich-Blake, 1975; Struhsaker, 1975) and by digital computer (Siniff and Jessen, 1969; Nicholls and Warner, 1972; Archibald, 1975; Harding, 1976). Such maps (Fig. 2), which

are called "activity spaces" by Weeden (1965), are more accurately termed *activity fields*.

The flexibility of machine computation permits rapid comparisons of activity fields with different quadrat sizes. While quadrat size could be selected for biological reasons (for instance, to approximate the area that might be scanned for resources from the position of a moving animal or to match the size of resource patches), it could also be chosen to allow direct comparisons between species or habitats.

Frequencies of quadrat use by radio-tracked red foxes (*Vulpes fulva*) and snowshoe hares (*Lepus americanus*) fit a zero-truncated negative binomial distribution (Siniff and Jessen, 1969). This distribution provides yet another method for

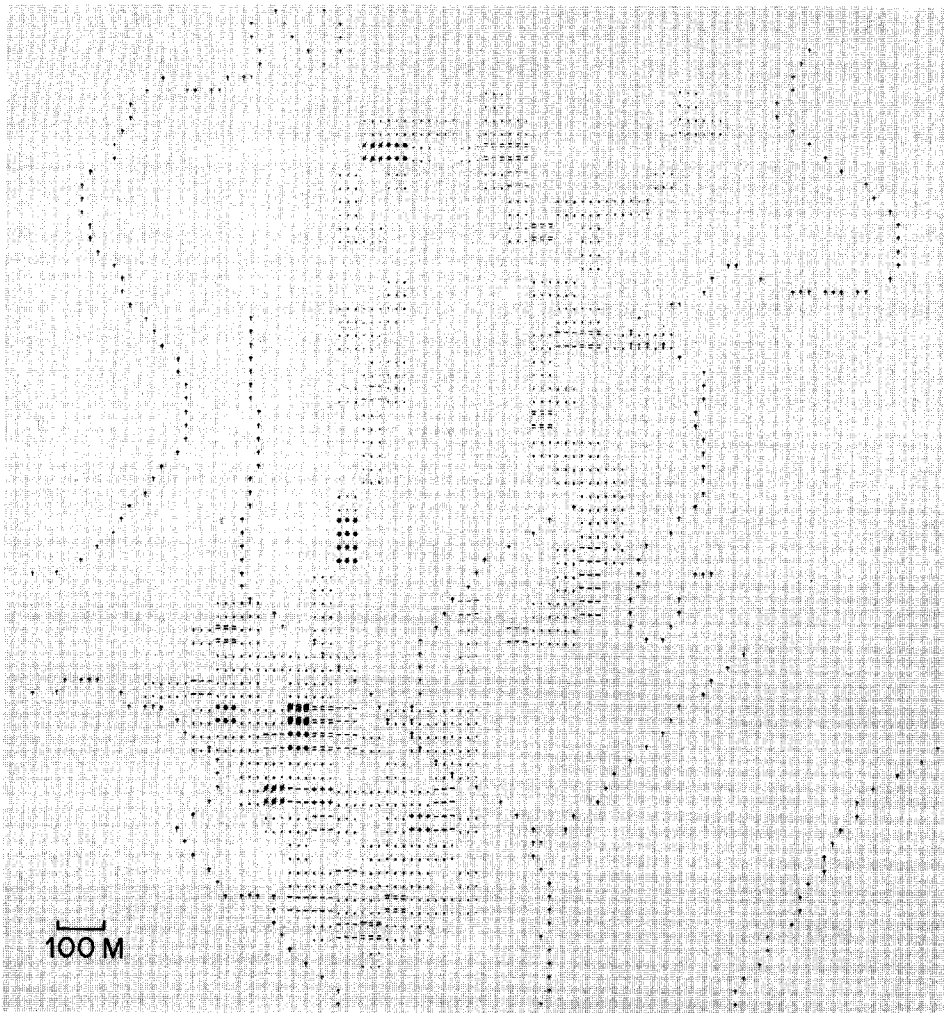


Fig. 2. Activity fields of one mangabey group over a 10-day period. Each block of characters represents a 50-m  $\times$  50-m quadrat, with optical density of characters proportional to the number of mangabeys sighted there during systematic half-hourly scan periods while the group was continuously followed. From Waser, 1976.

estimating the size of a home range, from the sum of expected quadrat frequencies, including the zero class, of the negative binomial distribution. More important, if a wide variety of species' activity fields are found to fit such a distribution, and if values of the distribution's parameters are (as Siniff and Jessen suggested) species-specific, its parameter  $k$  will provide a comparative index of clumping or nonrandomness of an activity field (Siniff and Jessen, 1969). Other candidates for such an index of nonuniformity of an activity field might include various statistics of environmental "grain" (Goodall, 1970; Pielou, 1969) or a simple statement of the fraction of total utilized area in which  $X$  percent of time is spent.

None of the analyses so far described preserves sequential information. Yet, among those parameters on which selection can act to increase efficiency of resource utilization, there are theoretical reasons to believe that movement sequence and rate are of particular importance (Cody, 1971, 1974; Schoener, 1971; Smith, 1974; Krebs, this volume). Given the distribution of an individual's locations in space, what are the "transition probabilities" for movements between these locations?

The simplest model of an animal's movements assumes that each movement to a new location is independent of all previous movements. Although animals seldom follow this assumption (Siniff and Jessen, 1969), the deviation of an animal's movements from those predicted by such first-order stochastic models can elucidate spacing patterns. For instance, the rate at which sequential locations of an individual tend to drift away from an initial position can be compared with that predicted for a random walk; the degree to which observations deviate from expectation provides an index of attachment to a home site (Waser, 1976). Some models of random walk incorporate changes in the probability of turns toward the home range center as distance from center increases ("centrally biased random walk"; Holgate, 1969; Rohlf and Davenport, 1969). More complex models can incorporate changes in the direction or rate of movement as a function of the animal's location. For instance, Beeler (1973) has investigated the potential movements of an imaginary worm crawling on a hexagonal lattice, whose choice of direction at each intersection of the lattice is dictated by rules depending on its previous "use" of the intersection.

Siniff and Jessen (1969) have taken a more pragmatic approach to the description of animal movements. Working with radio-tracked foxes and hares, the authors measured the distances traveled between sequential radio fixes and the relative angles between successive steps. Siniff and Jessen found these distributions to vary with species and habitat. Cody (1971) has tabulated similar distributions of step length and angle of turn for flocks of desert finches. He suggested that flocks both maximize coverage of areas within the home range and adjust the rates of return to given subareas to coincide with renewal rates of resources. Clutton-Brock (1975) has applied similar reasoning to the movements of red colobus (*Colobus badius*) feeding on growing shoots and leaves in East African forests. There are no precise measurements of rates of return for any animal.

In computer simulation of animal movements with either real or idealized distributions of step lengths and angles of turn, Siniff and Jessen concluded that these two parameters could produce activity fields statistically indistinguishable



from real data. Considering that their initial simulations explicitly ignored both the possibility of attachment to familiar sites and interactions with neighbors, it is not surprising that their simulations tended to produce activity fields that were less clumped and larger in area than those from which the data were originally obtained; but these differences were statistically significant in only a few simulations. The degree to which these simulations resemble actual activity fields underscores the possibility that an individual's movements, without reference to interactions with its neighbors, might in some cases account for the major characteristics of its activity field.

#### SPATIAL RELATIONS BETWEEN INDIVIDUALS

How are an individual's activity field and movements related to those of its neighbors? There are two basic approaches in answering such a question. One focuses on the simultaneous positions or movements of individuals, the other on the spatial relationships of individuals' activity fields.

Methods for measuring the instantaneous dispersion of individuals, particularly those based on nearest-neighbor distances, are readily extended from plants, for which they were developed (Clark and Evans, 1954, 1955), to sedentary animals or such bases of activity as anthills (Brian, Hibble, and Kelly, 1966), bird nest sites (Krebs, 1971), and mammalian or crustacean burrows (Lighter, 1975), or to moving individuals whose positions can be simultaneously recorded. For instance, Miller and Stephen (1966) applied these techniques to aerial photographs of sandhill cranes (*Grus canadensis*). By comparing the distribution of nearest-neighbor distances with that expected from a set of randomly positioned points, one can classify populations as *overdispersed* (when close spacing of individuals is less frequent than expected), *random*, or *aggregated* (when close spacing is more frequent than expected at random) (Hutchinson, 1953).

For most species, particularly when animals' movements are rapid and extensive or individuals are scattered or elusive, simultaneous location of numerous individuals is impractical. Groups of gray-cheeked mangabeys (*Cercocebus albigena*) in western Uganda, which occur at a density of less than 1 per km<sup>2</sup> in dense forest (Waser, 1976), provide an example. Yet, since large home ranges and poor visibility hinder not only an observer but also the animals' efforts to maintain exclusive use of a resource, data on spacing behavior in such species are of particular interest.

For gray-cheeked mangabeys, movements of two groups can in general be monitored only while groups are separated by less than 500 m. When groups are this close together (an unusual occurrence in this population), it is possible to record intergroup distances at regular time intervals.

From these data, the relative probabilities of approach or withdrawal can be calculated as a function of intergroup distance (Waser, 1976). A "radius of repulsion," if one exists, can be detected by statistical comparison of these probabilities with null probabilities of approach or withdrawal with respect to an arbitrarily chosen point or to a noninteracting neighboring group. For mangabeys, groups 2 km away and thus well beyond any possibility of interaction were

used to generate "null" probabilities. If it is difficult to observe more than one individual simultaneously, as is the case for mangabey groups, this straightforward approach is limited by small sample sizes, which result from just those low probabilities of close approach that constitute the phenomenon of interest.

These same data can also be tested against hypotheses predicting frequencies of encounters or approaches to a specified separation. A simple null hypothesis is that movements are independent and random. In this case, frequency of approach ( $Z$ ) to any specified distance ( $d$ ) can be computed from simple considerations of statistical mechanics for a two-dimensional perfect gas with density  $\rho$  and velocity  $v$ . When all individuals but one are stationary,  $Z = 2\rho v\sigma$ , where  $\sigma = d + s$  and  $s$  is the diameter of an individual (or group of individuals). If all individuals move at the same velocity  $v$ ,

$$Z = \frac{8\rho v\sigma}{\pi}$$

Such models can be extended to incorporate probability distributions of velocities, rather than constant  $v$ , or cases in which velocities of two individuals differ; in fact, however, predicted encounter frequencies are relatively insensitive to such refinements in the model.

Comparison of observed and expected frequencies of approach at given distances can determine whether or not avoidance occurs, as well as the radius of avoidance, if such exists (Waser, 1975b, 1976). When applied to mangabeys, this approach indicates that groups avoid each other at distances of several hundred meters, a conclusion supported by experiments that mimic intergroup encounters through the playback of specialized intergroup vocalizations (see section on "Communication of Advertisement and Threat").

The literature on primates frequently states an impression that groups avoid each other, so that "actual contact between groups is even less than expected" (DeVore and Hall, 1965, p. 36). Nevertheless, the data necessary to evaluate this hypothesis ( $\rho, v, d$ , and the observed frequencies of approach) are rarely reported (Table I). In fact, when such data are presented (or reasonable values can be inferred), in only one case does such a statement appear to be clearly warranted. For titi monkeys (*Callicebus moloch*), the null hypothesis predicts approach within 50 m approximately 6 times more frequently than intergroup confrontations actually occur (Mason, 1968). In contrast, according to the data presented by Schaller (1963), gorilla groups approach each other within 50 m 25 times *more* frequently than expected on the assumption that movements are independent. This result suggests a level of familiarity between groups that approaches the casual associations of chimpanzees.

Differences between observed and expected frequencies of approach might result either from a lack of independence or a lack of randomness of individuals' movements. In addition to tendencies to approach or avoid conspecifics, such factors as an avoidance of areas where previous encounters were lost or a concentration of activity in familiar areas could lead to such deviations. We return to these possibilities in the next section.

Only a few quantitative models are available for independent but nonrandom

movements. Jorgenson (1968a,b) has calculated the joint probability of quadrat occupancy assuming circular home ranges and neglecting all locations of an individual farther than its 95% recapture radius from its home range center. A potentially more general method, though requiring the assumption that activity fields can be described by bivariate normal distributions, has recently been developed by Dunn and Gipson (1977). Simultaneous movements of neighboring individuals were used to measure both home range overlap and canonical correlation of movements between neighboring individuals. These methods also provide expected distributions of interanimal distance given observed parameters of movement.

The spatial relationships of activity fields are another major concern in studies of individual's spacing. The simplest measure of the spatial relationships of activity fields is the percentage of an individual's home range overlapped by those of neighbors. In the case of the mangabeys described above, overlap was 72% for one group observed for a year. Such a measure is relatively straightforward to obtain, and methods exist for evaluating the probability of its deviation from the overlap expected if similar home ranges were randomly distributed in space (Metzgar and Hill, 1971). But such an overlap figure (1) is highly dependent on the observer's criteria for home range boundaries and (2) completely neglects differences in intensity of use of overlap areas. In many animals, overlap includes only those areas used occasionally (DeVore and Hall, 1965, describe a classic example among the primates). Thus arises the common conclusion that "core areas" do not overlap. In other cases, however, boundaries pass through areas of heavy use (Klopfer and Jolly, 1970).

Indices of overlap that take intensity of use into account include measures of overlap in the use of a spectrum of resources. These indices can serve just as well

TABLE I. OBSERVED AND EXPECTED RATES OF INTERGROUP ENCOUNTERS IN SELECTED PRIMATE SPECIES

Species	$\rho$	$v$	$\sigma$	Encounters/day	
	Groups/km <sup>2</sup>	m/day	m	Expected	Observed
<i>Cerecocebus albigena</i> (Waser, 1976)	.25	1,200	190	.15	.01
<i>Colobus badius</i> (Struhsaker, 1974)	5.92	649	100	.98	.59
<i>Colobus guereza</i> (Oates, 1974)	10.0	535	75	1.02	.73
<i>Papio anubis</i> (Harding, 1973)	.15	5,000	300 <sup>a</sup>	.57	.30 <sup>b</sup>
<i>Gorilla gorilla</i> (Schaller, 1963)	.14	532	100 <sup>a</sup>	.02	.26 <sup>b</sup>
<i>Callicebus moloch</i> (Mason, 1968)	131.00	635	75 <sup>a</sup>	15.89	1.4

<sup>a</sup>These studies do not provide precise values of  $\sigma$ , but estimates of probable group spread and mean distance at which "encounters" occurred are possible from the data presented.

<sup>b</sup>Rates of encounter/day were calculated as total (encounters/total observation hours)  $\times$  (10 hours observation/day).

for studies of spacing, with quadrats substituted for resources. A numerically simple index was suggested by Holmes and Pitelka (1968; see also Schoener, 1968a; Baker and Baker, 1973):

$$O_{ij} = 1 - 1/2 \sum_a |P_{ia} - P_{ja}| \quad (1)$$

where  $O_{ij}$  is the index of overlap between individuals  $i$  and  $j$ ,  $P_{ia}$  is the probability of use by  $i$  of quadrat  $a$ , and  $P_{ja}$  is the probability of use by  $j$  of quadrat  $a$ . Alternative measures of resource overlap include one derived from information theory (Horn, 1966; Morse, 1970) and several from competition coefficients ( $\alpha$ ), which are in fact measures of overlap in resource use (Colwell and Futuyma, 1971; May, 1975). May argues on mathematical grounds in favor of Pianka's (1975) measure:

$$O_{ij} = \frac{\sum_a P_{ia}P_{ja}}{\sqrt{\left(\sum_a P_{ia}^2\right)\left(\sum_a P_{ja}^2\right)}} \quad (2)$$

However, the shortcomings of other formulations, as discussed by May, do not appear to apply to studies of overlap in space. The relative merits of the various indices as measures of spatial overlap remain to be worked out. The only index of overlap so far used for intensities of quadrat use is the product-moment correlation coefficient of the frequencies of use by animals  $i$  and  $j$  in all quadrats used by either animal (Adams and Davis, 1967); this correlation coefficient is identical in form mathematically to equation (2), with  $(P_{ia} - \bar{P}_i)$  and  $(P_{ja} - \bar{P}_j)$  substituted for  $P_{ia}$  and  $P_{ja}$  respectively.

The degree to which any of these measures of spatial overlap estimate competition between individuals depends on the relationship between the renewal periods of resources in each quadrat and the time intervals between visits to those quadrats by different individuals. The latter can be estimated by repeated sampling of short-term overlap (see Schoener, 1970), but so far no attempts have been made to measure this parameter.

Just as information about an animal's movements is lost by reducing its activity field to a single parameter, such as area or  $k$  from the negative binomial distribution, information about spatial relationships is lost by reducing an individual's isolation field to an index of overlap. Determination of an individual's isolation field follows directly from determinations of all overlapping activity fields. Thus, all of the considerations discussed above for the measurements of activity fields apply equally to isolation fields. In particular, the observer must choose an appropriate quadrat size and decide whether continuous recording, instantaneous sampling at regular intervals, or trapping will optimize the balance between feasibility and accuracy in describing an individual's probability of occupying the specified quadrats. In addition, because an isolation field expresses a relationship between individuals, isolation fields with respect to different sets of opponents often differ (see the next section).

Although almost no measurements of isolation fields are now available, it is

clear that isolation varies a great deal even among species with territorial behavior, in the sense that individuals attack or dominate intruders within a fixed area. Anecdotal observations suggest that many territorial species have isolation fields with pronounced convexity with respect to the center of the individual's range. The isolation fields of territorial dwarf cichlids (*Apistogramma ramirezi*) in a large aquarium illustrate this pattern (Black and Wiley, 1977). In cross-sections halfway through four individuals' isolation fields (Figure 3), the values of each individual's isolation ratio are a convex function of distance from the center of its range. Some territorial species lack such strong convexity in their isolation fields (see Wiley, 1973). For example, bicolored antbirds (*Gymnophithys bicolor*) (Willis, 1967), mentioned earlier, and Steller's jays (*Cyanocitta stelleri*) (Brown, 1963) seem not to occupy any areas with high isolation ratios. Even ovenbirds (*Seiurus aurocapillus*), long thought to occupy exclusive areas, wander extensively within neighbors' areas (Zach and Falls, in press). This unobtrusive trespassing was detected only by carefully following marked individuals in early spring before foliage had grown enough to interfere with observations. Zach and Falls's data suggest that isolation ratios for a territorial ovenbird are high, but probably do not reach 1.0, near the center of its territory and decrease gradually away from the center (Figure 4). Thus, even though ethologists and ecologists have seldom measured isolation

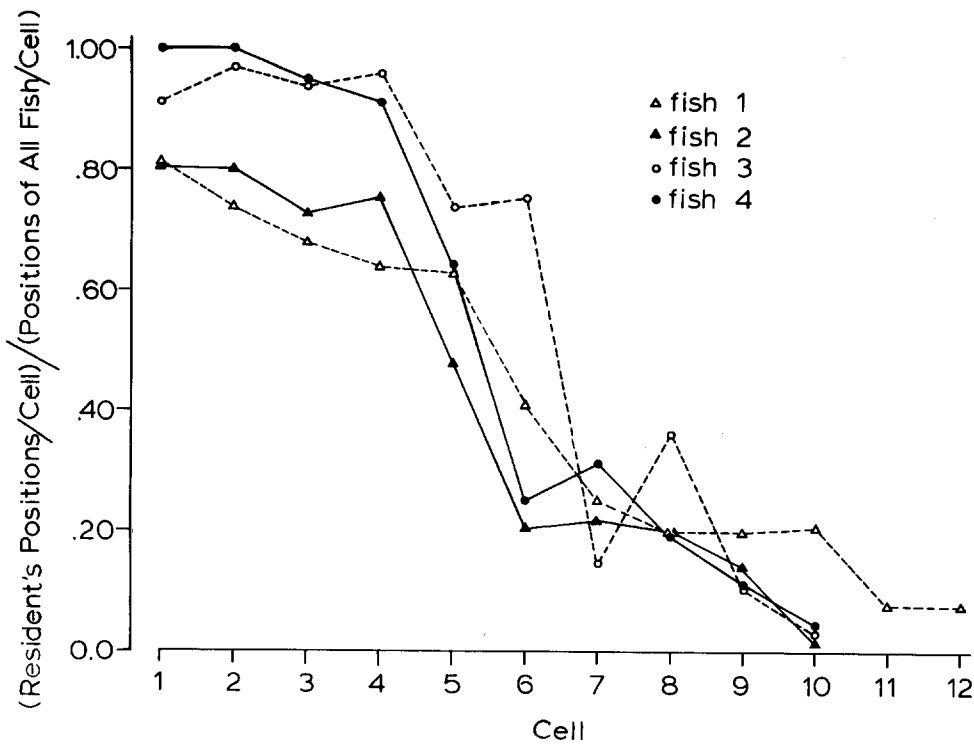


Fig. 3. Cross-sections halfway through four residents' isolation fields for the dwarf cichlid *Apistogramma ramirezi* in a large aquarium. Ordinate, isolation ratio (see text). Abscissa, 5-cm<sup>2</sup> quadrats along an unobstructed corridor from the center of an individual's territory to the periphery. From Black and Wiley, 1977.

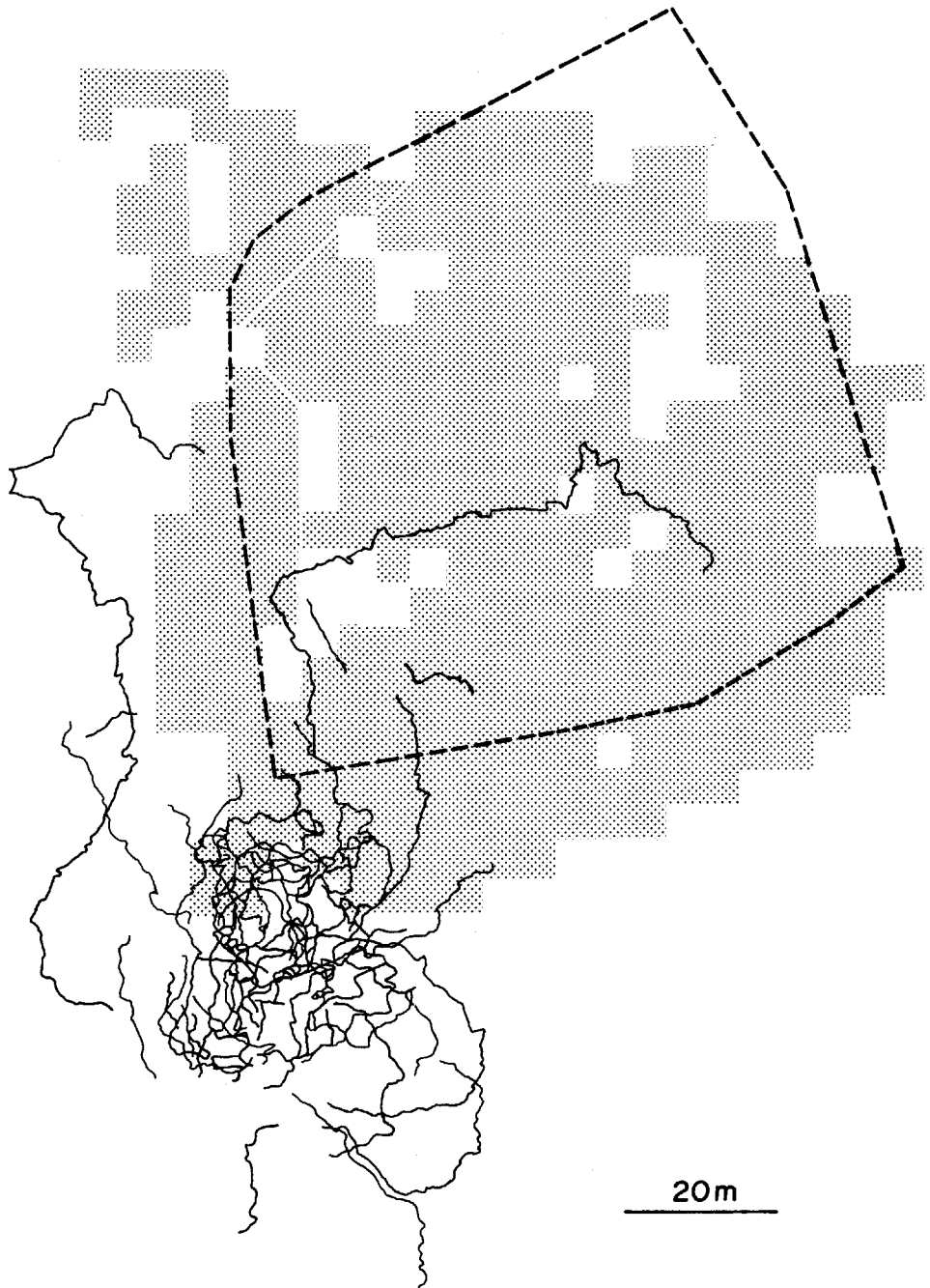


Fig. 4. Trespassing of male ovenbirds into neighboring territories. Shaded area: area used in foraging by Male 5. Dashed line: boundary of Male 5's "song territory" (minimum convex polygon surrounding all song perches). Solid lines: foraging paths of Male 6, Male 5's neighbor. From Zach and Falls, in press.

fields, it is clear that species differ considerably in this regard, even among species with at least superficially similar patterns of aggression.

In the past, ecologists and ethologists have debated whether the essence of territoriality was site-dependent dominance or exclusive occupation of an area, in other words, characteristics either of spatial variation in aggression or of isolation fields. We propose to abandon the search for a unitary definition of territoriality and any simple dichotomy between territorial and nonterritorial species. Instead, we shall address the variation among species in relationships of aggression, isolation, and activity fields, first by considering the behavioral mechanisms that control these relationships (in the next two sections), then by considering the selection pressures that can explain their evolution (in the fourth section).

## BEHAVIORAL MECHANISMS OF SPACING

The behavioral mechanisms that control spacing have to explain the causal relations among an individual's activity field, isolation field, and agonistic tendencies (its tendencies to approach, avoid, threaten, and attack) for each category of opponents. There has never been a systematic review of the possible behavioral mechanisms of spacing or variation in these mechanisms among species. This section integrates evidence from laboratory and field in order to make a start in this direction. Many of the phenomena discussed here have clear implications for the evolution of spacing behavior, but we confine our discussion in this section to the proximate relationships between spacing behavior and pattern. This section treats mechanisms of spacing; subsequent sections consider evolutionary adaptations.

We emphasize that ethology has much yet to learn about the determinants of spatial variation in agonistic tendencies and its causal relationships with activity and isolation fields. Rather than attempt to reach definite conclusions, our discussion has two goals: (1) to systematize hypotheses about the behavioral mechanisms that can generate patterns of spacing, so that future studies might succeed more often in discriminating among the possibilities; and (2) to indicate the relevance of laboratory studies of aggression and dominance to the control of spacing behavior in natural populations.

Before proceeding, it is important to dispel two oversimplifications. First, agonistic tendencies in encounters do not completely determine individuals' isolation fields. One additional factor is the probability that individuals will detect each other's presence. This probability, like agonistic tendencies, might well vary with an opponent's location or proximity. As a consequence, *frequencies* of aggressive encounters are not necessarily good indices of aggressive *tendencies*. For instance, consider the inverse relation between the frequency of aggression between territorial neighbors and the sizes of their territories (van den Assem, 1967; Post, 1974). Individuals on smaller territories would presumably detect each other's presence near a boundary more frequently; thus, situations evoking agonistic behavior would occur more frequently. Two separate variables are involved: the frequency of encounters and behavioral tendencies during encounters. This

section will focus on agonistic tendencies after detection of an opponent; the third section will return to the problems of detection.

Second, similar patterns of spacing can result from different behavioral mechanisms. Although exclusively occupied areas are often interpreted as evidence for site-specific defense, different mechanisms can generate exclusive areas. To pick an extreme case, extensive isolation could simply result from wide separation of patches of resources or suitable habitat. Traveling to a distant patch on the chance of using some of it might not be energetically profitable even in the absence of defense by another individual. For instance, mangabeys occupy exclusive areas where unsuitable habitat partially delimits their home ranges (Chalmers, 1968a; Waser, 1976) but not, apparently, where suitable habitat is continuous (Cashner, 1972). Other possible examples of such constraints on spacing include certain marmots (*Marmota*) (Barash, 1973) and talapoin monkeys (*Miopithecus talapoin*) (Gautier-Hion, 1971). Thus, direct responses by individuals to the distribution of resources might explain their spatial relationships.

Similar spacing patterns could also result from different balances between aggression and avoidance (Marler, 1976). Zoologists have focused on animals' tendencies to threaten and attack conspecifics rather than on their tendencies to avoid them. Yet, avoidance is clearly an important component of spacing behavior (see "Reactions to an Opponent's Proximity" below). Because the dominance relationship between two individuals at a particular location depends on their relative agonistic tendencies there, a change in dominance relationship could result from changes in either tendencies to approach and threaten or tendencies to withdraw. Largely exclusive territories could result not only from tendencies to attack and supplant other individuals in the center but not near the periphery, but also from each individual's tendencies to avoid others in the periphery but not in the center of its range.

#### REACTIONS TO AN OPPONENT'S PROXIMITY

The behavioral mechanisms that regulate the dispersion of activity fields and the nature of isolation fields often hinge on spatial variation in agonistic tendencies. Before addressing variation in aggression with location, however, we first consider reactions to the proximity of opponents. Our discussion will indicate that changes in agonistic tendencies with an opponent's proximity have important consequences for the likely simultaneous positions of individuals but cannot alone generate overdispersed activity fields.

Early ethologists noted that individuals of many species tended to maintain characteristic separations by means of threat and avoidance at closer distances (Hediger, 1950). These individual distances are particularly noticeable in animals that gather in flocks or herds (Emlen, 1952; Crook, 1961). Marler (1955a,b, 1956b, 1957) measured changes in the probability of agonistic interactions as a function of the separation between chaffinches (*Fringilla coelebs*) feeding from movable hoppers in aviaries. His experiments, conducted during the autumn and



winter, when chaffinches normally forage in flocks, were the first to measure variation in agonistic behavior with proximity of opponents. He established that the frequency of aggression increased as separation decreased. At any separation, males were more aggressive toward other males or toward females disguised with male coloration than toward normal females.

Variation of agonistic tendencies with the separation between opponents is probably a general phenomenon. Male fiddler crabs (*Uca terpsichores*) increase their rate of claw-waving in response to a test stimulus (a tethered crab) as the stimulus distance decreases (Zucker, 1974). The response of groups of gray-cheeked mangabeys to the playback of a call used in intergroup spacing depends strongly on their distance from the playback speaker (Figure 5) (Waser, 1975a).

Does spacing in natural circumstances ever result from agonistic tendencies that vary solely with separation between opponents? Evidence that individuals avoid each other without relation to their locations is available for mangabeys and for cheetahs (*Acinonyx jubatus*). The tendency of mangabey groups to move away from spacing calls of other groups within a few hundred meters does not depend on the group's location in the home range; groups showed no significant differences in responses at their home range center and periphery (Waser, 1975a). Moreover, there is no preference for retreat toward the center of the group's range. Observations and experiments also confirm that mutual long-distance avoidance occurs without respect to the relative sizes of interacting groups.

Groups of cheetahs also avoid each other at a distance, although persistent olfactory signals rather than long-range acoustic signals mediate the interactions (Eaton, 1970). Observations of cheetahs' natural movements suggest that the locality at which an individual contacts another's trail does not influence its immediate reaction. Adult males in small bisexual groups leave olfactory marks by directional urination every 30–100 m as the groups move. When a group detects another's mark, they tend to spread out until a second mark is located and then depart approximately at right angles to the predecessors' trail. The urine marks evoke reactions from later groups for about 24 hours after deposit. This study, however, could not eliminate the possibility that the locations of olfactory contacts might have some influence on the followers' subsequent direction of movement or that marking might differ in frequency in different parts of a group's range.

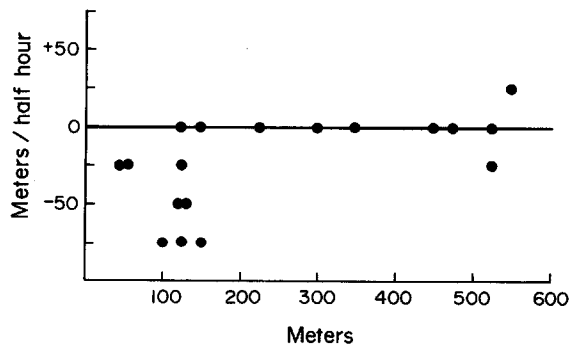


Fig. 5. Net change in rate of movement of mangabey groups as a function of the distance from site of spacing-call playbacks to nearest individual in the group. From Waser, 1976.

Mutual avoidance of other individuals or their signs, without regard to the location of encounters, generates "time-plan" dispersion (Leyhausen and Wolff, 1959), in which at any instant an individual is unlikely to have others nearby. If, in addition, individuals practiced long-term avoidance of areas in which contacts with others were too frequent, then site-independent avoidance could generate regularly spaced activity fields or even exclusive areas. The spacing of feral house cats, mangabeys, and cheetahs might indeed illustrate these conditions (Leyhausen and Wolff, 1959; Eaton, 1970), although the arrangement of activity fields and the nature of isolation fields need further study in these species.

Regular dispersion of activity fields in suitable habitat characterizes populations from diverse taxa, including pumas (*Felis concolor*) (Hornocker, 1969), antbirds (*Gymnophrys bicolor*) (Willis, 1967), American robin (*Turdus migratorius*) (Young, 1951), and lizards (*Uta stansburiana*) (Tinkle, 1965). Overdispersion of activity fields may persist even when overlap is extensive, as in olive baboons (*Papio anubis*) in Nairobi National Park, Kenya (DeVore and Hall, 1965). Mutual avoidance without regard to location, in combination with long-term avoidance of areas in which other individuals or their signs are frequently encountered, could theoretically produce such patterns, but regular spacing usually results from some pattern of variation in agonistic tendencies with location.

Agonistic behavior that varies solely with the separation between opponents would be sufficient to generate overdispersed territories in one special case: small territories that residents can survey in their entirety from habitual locations. Nesting black-headed gulls (*Larus ridibundus*) exemplify this situation. Patterson (1965) has shown that the tendencies of a resident to attack or threaten a strange intruder depend entirely on the intruder's distance from the resident's current location rather than its distance from the resident's nest or habitual perch. Resident gulls maintain nearly exclusive territories because each usually perches at a "station" near the center of its small territory. Thus, an intruder near the center of the territory is also usually near the resident.

Effects of proximity and location on aggression can interact, as during the transition from winter flocks to spring territories in certain passerine birds. Often, an individual establishing a territory first localizes its activities around certain preferred singing sites, and then the distance at which opponents evoke aggression gradually increases (Conder, 1949, 1956; Marler, 1956a,c). Eventually, the resident's agonistic tendencies come to depend more on the location of an encounter with an intruder than on the intruder's proximity. There are, however, no quantitative studies of this interaction of location and proximity in determining a territorial resident's agonistic tendencies.

In conclusion, when individuals' activity fields are overdispersed, with less overlap than predicted for randomly positioned activity fields, the spacing of activity fields and the form of individuals' isolation fields often develop from some pattern of spatial variation in the individuals' agonistic tendencies. To generate such overdispersion, individuals both evoke withdrawal by others from specific areas, either by employing long-range or persistent signals or by directly challenging intruders, and avoid individuals or their signs in other areas.

In the earliest accounts, a territory was recognized as the locus of positions in which the resident won agonistic encounters. When territorial individuals met opponents beyond this locus, they either reliably "lost" or the outcome was less predictable, depending on whether the opponent was within its territory or not (Howard, 1920; Nice, 1941). Site-specific dominance has subsequently become an explicit criterion for territoriality (Emlen, 1957). Beginning with Huxley's (1934) analogy between a bird's territory and a rubber disc, permitting limited contraction under external pressure, ethologists have proposed that a territorial resident's aggressiveness decreases away from the center of its territory (Fitch, 1940; van Iersel, 1958; Tinbergen, 1960; Harris, 1964; van den Assem, 1967).

In documenting such spatial variation in agonistic tendencies, one must carefully distinguish between the *frequencies* of agonistic encounters and each individual's behavioral *tendencies* during encounters. Evidence for spatial variation in agonistic tendencies requires studies of an individual's responses to similar opponents in different locations. For example, laughing gulls (*Larus atricilla*), which defend nesting territories within a colony, react less frequently with threats and chases as the distance of an intruder from the subject's nest increases (Burger and Beer, 1975). In three-spined sticklebacks (*Gasterosteus aculeatus*), standard opponents evoke progressively less aggression from a territorial male the farther the opponent is from the resident's nest (van Iersel, 1958).

Experiments with playbacks of tape-recorded vocalizations have suggested that several species of territorial passerines respond more intensely to playbacks from the center of their territories than to playbacks of the same stimulus from the periphery (Dhondt, 1966; Ickes and Ficken, 1970; Brooks and Falls, 1975). However, a difference in average responses to playbacks in central and peripheral positions might also arise if subjects were less likely to detect a peripheral stimulus promptly. Definite confirmation of an effect of the location of playback on aggressive tendencies might involve examining the subjects' responses after approaching the speaker or, even better, locating the subject before each playback in order to control for the initial distance between the subject and the speaker.

Observations of site-dependent dominance in the field also suggest that individuals' agonistic tendencies vary with location. A number of these studies have focused on territorial passerines that reside year round near their breeding areas but range more widely during winter months than during the breeding season. Territorial Steller's jays (*Cyanocitta stelleri*) during the winter become progressively lower in rank at feeding stations as they move farther from the locations of their breeding territories (Brown, 1963). Other examples are birds specialized for feeding at swarms of army ants in tropical forests. Individuals frequently must travel considerable distances to find a swarm on any particular day. Among bicolored antbirds (*Gymnopithys bicolor*), each pair has an area within which it dominates all other conspecific individuals at ant swarms, and each individual's rank drops the farther it is from this territory (Willis, 1967, 1972). An example of a mammal with site-dependent dominance is the chipmunk (*Tamias*

*striatus*) (Dunford, 1970). In this species, an individual's area of dominance corresponds to the central portion of its range.

Variation with location in an individual's aggression toward opponents suggests a third function of spatial coordinates, in addition to activity and isolation fields, with special relevance for the behavioral control of spacing: an *aggression field*. We can define this field as the value of some measure of an individual's agonistic tendencies in encounters with specified opponents at different locations. As we have seen, an individual's agonistic tendencies toward an opponent often vary with its proximity to the subject as well as its absolute location. The concept of an aggression field is best restricted to variation in a subject's agonistic tendencies with an opponent's absolute location, when proximity to the subject is controlled. In this sense, the concept serves to emphasize the special importance of this aspect of agonistic behavior for the behavioral mechanisms that regulate spacing.

No aggression field has ever been measured in any detail. Perhaps van Iersel (1958) came closest when he determined the decline in aggressiveness of male sticklebacks toward standard opponents as distance from the subject's nest increased. Van den Assem (1967) called this function an "aggression gradient." Patterson (1965) and Burger and Beer (1975) obtained similar measurements for nesting gulls.

Accurate measurement of an individual's aggression field might encounter a difficulty not met with activity and isolation fields. If an individual's tendencies to attack and avoid do not strongly covary across locations, no aggression field of a single variable can completely describe spatial variation in an individual's tendencies in encounters. Nevertheless, the available observations in natural situations suggest, as a good first hypothesis, that a single variable can often describe changes with location in an individual's agonistic tendencies toward specified opponents.

Variation in agonistic tendencies with location might result from any one, or a combination, of three influences on agonistic behavior, considered in turn below: effects of familiarity with the site of an encounter; effects of previous experience at the site of an encounter; and effects of external referents for aggression. These effects have received considerable attention in experimental studies, but their importance for spacing in natural populations has had no systematic appraisal.

**LOCATION EFFECTS AS A RESULT OF DIFFERENTIAL FAMILIARITY WITH THE ENCOUNTER SITE.** The predictable polarity in the interactions of intruders with residents in their territories was early attributed to the psychological advantage of the individual on familiar ground (Howard, 1920; Nice, 1941). Familiarity with the site of an encounter has such a strong effect on an encounter's outcome that it is standard practice to control this variable in experimental studies of aggression. Early experiments with fish, lizards, doves, and mice have established that prior residence in an enclosure confers an advantage, often insurmountable, in encounters with intruders (Evans, 1936; Ulrich, 1938; Diebschlag, 1941; Guhl and Allee, 1944; Braddock, 1949; Baerends and Baerends-van Roon, 1950; Ritchey, 1951). Recently, Zayan (1975, 1976) found for platyfish (*Xiphophorus*) hybrids that prior residence in an aquarium for three hours was sufficient to establish an individual's dominance over subsequently introduced individuals.

In natural circumstances as well, prior residence often confers dominance. For instance, among tits of several species of *Parus*, individuals gather in winter flocks in which the highest-ranking individual is the male whose previous breeding territory is included in the flock's range. Sometimes, this male's area of dominance is greater in winter than during the breeding season, so that he comes to dominate during the winter his former territorial neighbors (Dixon, 1963, 1965; Hartzler, 1970; Glase, 1973). In addition, chickadees transported to a new area become subordinate to the resident individuals (Odum, 1941), although this result does not separate effects of unfamiliar opponents from effects of an unfamiliar location.

It seems probable that this effect of familiarity with the site of an encounter on aggressive tendencies is related to the effects of novel environments on exploratory and "emotional" or "fearful" behavior. A recent experiment with territorial jewelfish (*Hemichromis bimaculatus*) (Heuts and Boer, 1973) suggests this connection. When transferred to a new aquarium, the fish tended to establish their new territories in close relationship to conspicuous objects that resembled those in their previous territories. These results, however, do not allow us to separate the individual's tendencies to remain near familiar objects from the effects of those familiar objects on their agonistic tendencies.

The connection between reactions to novel environments and aggressiveness has received only intermittent attention, in spite of some interesting results. Mice bred for lower defecation rates in novel environments (an indication of "fearful" or "emotional" behavior) are also more aggressive (Hall and Klein, 1942); conversely, mice bred for aggressiveness have lower defecation rates in a novel environment (Lagerspetz, 1961). For the fish *Trichogaster trichopterus*, prior residence in an aquarium, which predisposes an individual to dominance over others introduced later, reduces indications of fear but does not increase aggression (Frey and Miller, 1972). Tendencies to avoid strong stimuli, including threatening conspecifics, in novel circumstances would have clear relevance for spacing behavior.

The effects of prior residence on agonistic tendencies can result in territories of different sizes, depending on whether or not individuals establish themselves simultaneously. To obtain the maximum number of territorial individuals in experimental situations, usually small fish in large aquaria, the investigator must introduce all individuals into the enclosure simultaneously (see van den Assem, 1967). When individuals are introduced sequentially, those with precedence are able to exclude latecomers from much larger areas. Knapton and Krebs (1974) have documented a similar phenomenon in wild song sparrows (*Melospiza melodia*). Populations are denser when a habitat is settled synchronously rather than asynchronously. In this case, however, the latecomers are also younger individuals. Maynard Smith (1974a) presented a formal model of this effect of synchrony in territory establishment.

**LOCATION EFFECTS AS A RESULT OF PREVIOUS ENCOUNTERS AT THE SITE.** The value of an individual's aggression field might be expected to correlate point by point with the value of its activity field for two reasons: (1) as discussed above, an individual's familiarity with any location, as determined by the intensity of its use,

affects its dominance there; or (2) it might avoid locations where it had previously lost encounters. The two possibilities are not mutually exclusive. In the early stages of territory establishment, chance differences in the values of the activity field in the zone of overlap might influence the outcomes of encounters there; if neighbors tended to avoid locations where they had lost encounters, the centers of their activity fields might subsequently shift farther apart.

A lasting tendency to avoid sites of low dominance would also explain the persistence of boundaries during the replacement of a territorial resident by a newcomer. In such circumstances, the newcomer often comes to have nearly the same boundaries as its predecessor (for instance, Owen-Smith, 1975; Wiley, 1973), so that boundaries in a population of territorial individuals become traditional. There are no experimental studies of the mechanisms that maintain such traditions in the locations of boundaries.

**EXTERNAL REFERENTS FOR AGONISTIC TENDENCIES.** Proximity to external referents, such as mates, nests, or critical food sources, can also influence an individual's agonistic tendencies at a particular location. The importance of proximity to an external referent is especially clear when the referent moves. For parents of many species, their young serve as external referents for threat and attack when conspecifics approach too close. In many species, protection of young is the primary determinant of aggressive behavior by females.

In species that form pair affiliations, partners often direct aggression or threat to nearby individuals other than the partner. This phenomenon has been variously interpreted as defense of the mate, redirection of aggressive tendencies evoked by proximity to the mate, and coupling between the motivational systems of aggression and sexual behavior. Among wildebeest (*Connochaetus taurinus*), as in many other ungulates, males in sedentary populations maintain exclusive mating rights within fixed areas to which they attempt to attract female herds, but in some migratory populations, wildebeest males attempt instead to set up temporary exclusive areas with respect to the locations of females rather than fixed spatial referents (Estes, 1969; Jarman, 1974). In many primates and ungulates, males form consort relations with estrous females and attack other males that approach too closely.

Tree squirrels of the genus *Tamiasciurus* demonstrate another possible relationship of agonistic tendencies to mates as an external referent (Smith, 1968). Both sexes maintain largely exclusive territories throughout the year. During the mating season, several males enter the territory of an estrous female on the one day that copulations occur. During this day, females relax their aggressive tendencies toward intruding males. One male quickly establishes its dominance over the others and then follows the female closely, except for forays to chase other approaching males.

Individuals of the opposite sex sometimes are external referents for agonistic tendencies even when individuals occupy stationary territories. A male yellow-hooded blackbird (*Agelaius icterocephalus*), for instance, is more likely to attack or threaten a strange male near the periphery of its territory or even in neighbors' territories when the stranger has closely approached a female. Males of this neotropical species maintain territories in marshes and attract a succession of

females to nest in their territories. During the three to four days immediately preceding egg laying by one of a male's mates, he becomes aggressive even toward other females within several meters of the mate (Wiley, personal observation).

The effects of females on agonistic interactions between males have received surprisingly little experimental investigation. In domestic mice, the presence of a female or odors from females reduce fighting between males (Fredericson, Story, Gurney, and Butterworth, 1955; Mugford, 1973). Prior sexual experience reduces a previously naive male's aggression in a subsequent encounter with another male four days later (Lagerspetz and Hautojarvi, 1967). In laboratory colonies of wild rats (*Rattus norvegicus*), males do not usually fight in the presence of an estrous or proestrous female, but males do begin to fight after a female leaves them (Barnett, 1963) or when two or more males visit a site marked by an estrous female (Calhoun, 1962).

In contrast, recent experiments with zebra finches (*Taeniopygia guttata*) have shown that a male's aggression toward a male partner increases dramatically in the presence of a female (Caryl, 1975). The effectiveness of the stimulus female declines sharply with her distance from the two males. In comparison with a strange female, a male's mate has a slightly greater effect on his aggression toward a male partner. These effects seem likely to increase the spacing of males near females.

A den, a nest, or localized food also often serves as an external referent for an individual's agonistic tendencies. For instance, aggression within a group of mangabeys increases tenfold when they exploit the basketball-sized fruits of *Treculia* (Chalmers, 1968b), an effect repeatedly noted in studies of artificially provisioned primates (Wrangham, 1974). This effect of concentrated food sources is taxonomically widespread; coconut crabs *Birgus latro* have an elaborate repertoire of agonistic behaviors displayed on encounters at opened coconuts (Hel, 1975). Aggressive behavior near concentrated food in some cases could result entirely from the proximity of individuals in these circumstances, but in mangabeys, coconut crabs, and other cases, the presence of concentrated food evokes aggression when similar proximity of individuals in other circumstances does not.

The converse of this situation is demonstrated by cases of low aggression in the absence of a referent. Oates (1976) found that the normally aggressive relationships between groups of black-and white colobus (*Colobus guereza*) can break down when these normally arboreal, leaf-eating monkeys visit small ponds to forage on aquatic vegetation; ranges of many otherwise territorial groups overlap at this location, and groups intermingle peacefully. In baboons and vervets, aggressive interactions are often suppressed at waterholes, which represent spatially limited but not ecologically limiting resources (S. Altmann, 1974; DeVore and Hall, 1965; Struhsaker, 1967).

In species that show little agonistic behavior of other sorts, individuals still frequently attack or threaten conspecifics at the nest or den. In one experiment to determine the influence of nests on an aggression field, the nests of female red-winged blackbirds (*Agelaius phoeniceus*) were moved to new locations near or across the original male's boundary (Nero and Emlen, 1951). Males did not expand their territories to include the new positions of their mates' nests, perhaps because red-

winged blackbirds lack strong associations with their mates once the females begin incubation. In contrast, studies of a tropical congener, the yellow-hooded blackbird, suggest that changes in activity fields, and subsequent changes in aggression fields, follow shifts in the location of active nests in a male's territory (Wiley, personal observation). In this species, unlike red-winged blackbirds, the male constructs the nests in his territory.

The influences of external referents on individuals' agonistic tendencies probably include avoidance of other individuals' referents. For instance, male common grackles (*Quiscalus quiscula*) seldom closely approach females accompanied by other males (Wiley, 1976a). Male hamadryas baboons (*Papio hamadryas*) refrain from challenging one another for females associated with another male (Kummer, Götz, and Angst, 1974). Somewhat analogous is the "protected threat" of many primate species, which depends on avoidance by the threatened individual as a result of the presence of another, referent individual.

Proximity to an external referent, such as a particular female or nest, presumably both increases one individual's aggressive tendencies and reduces the other's. In the defense of a mate or young, the relevant distance that influences an individual's aggression is probably that between the referent and the opponent, while protected threat probably depends on the distance between an individual and the referent. However, no experimental studies have yet documented the variation in agonistic tendencies with changes in the pertinent separations between subject, referent, and opponent.

In conclusion, the proximate control of spatial variation in an individual's agonistic tendencies includes effects of (1) the individual's proximity to opponents; (2) its proximity to external referents for aggression; (3) its opponent's proximity to such referents; and (4) its familiarity with the location and previous experience in agonistic encounters there. The determinants of an individual's activity field and its aggression field are likely to have reciprocal effects on each other.

#### INDIVIDUAL AND POPULATION DIFFERENCES IN AGONISTIC TENDENCIES

The preceding sections have examined the interactions among an individual's agonistic tendencies, its spatial relationships with opponents and external referents, and its familiarity with different locations. The available literature, for the most part, documents these interactions only vaguely. Nevertheless, it is clear that both spacing and agonistic behavior vary with age and season for any one individual and among populations and species.

Physiological, genetic, and experiential determinants of these differences remain largely unexplored. Endocrine and genetic differences with sex, age, and season, which have extensively documented effects on dominance and aggressiveness in laboratory situations, are almost certainly associated with these same differences in agonistic behavior under natural circumstances. In one of the few attempts to administer steroid hormones to animals in natural circumstances (Emlen and Lorenz, 1942), results dramatically matched naturally occurring



changes in agonistic behavior and interanimal spacing. In this case, implants of an androgen in male valley quail (*Lophortyx californicus*) during the winter resulted in prompt increases in aggressive behavior by the implanted birds in their covey and, within a few weeks, their separation from the covey, behavior that normally coincides with the start of breeding activity in the spring. Individual differences in agonistic tendencies depend in complex ways on differences in hormone levels and previous social experience. Androgen levels and success in territorial interactions can mutually reinforce each other (Bramley and Neaves, 1972).

**EFFECTS OF PREVIOUS EXPERIENCE.** One effect of social experience that might influence spacing behavior is a change in agonistic tendencies as a result of the frequency of interactions in a preceding period. In laboratory rodents, isolation induces increased aggression in tests with pairs of isolated males (Valzelli, 1969; Banerjee, 1971; Spencer, Gray, and Dalhouse, 1973). Incidence of aggression by such pairs increases with the duration of isolation. Conversely, aggression eventually decreases between isolated mice subjected to repeated tests at approximately weekly intervals (Banerjee, 1971). Isolation of hermit crabs (*Pagurus samuelis*) similarly increases an individual's dominance, its probability of initiating aggression, and its frequencies of high-intensity aggressive actions in tests with group-held opponents (Courchesne and Barlow, 1971). After a period of deprivation from any opportunity to see rivals, damselfish (*Microspathodon chrysurus*) spend more time in a small chamber with a view of a rival (Rasa, 1971). Since the subjects performed normal aggressive displays in the chamber when in sight of a rival, Rasa concluded that the amount of time spent in the small chamber was a measure of the subject's readiness to fight.

Other experiments have led to the opposite conclusion: isolation from opponents reduces aggressiveness. For example, when hermit crabs (*Clibanarius* species) are held at high or low densities (17 and 35 cm<sup>2</sup>/crab) for a week, those with experience of low densities retreat from opponents at nearly twice the distance as those from high densities. Consequently, crabs from low densities lose most of their encounters with opponents from high densities (Hazlett, 1974). In another example, the cichlid *Haplochromis burtoni* becomes less aggressive toward small, blinded stimulus fish after being deprived of normal opponents (Heiligenberg and Kramer, 1972).

Two basic parameters of these experiments have received little systematic attention: the specificity of the deprived stimulation and the specificity of the effects for different responses or stimulus preferences. For instance, "isolation" in most experiments involves deprivation from all stimulation except a bare cage. In these circumstances, mice become hyperreactive and hyperkinetic (Valzelli, 1969; Banerjee, 1971). Are changes in aggressiveness the primary effects of such deprivation? Does contact with partners of different sex or age have different tonic effects on aggressive tendencies? Is exposure to conspecifics without contact as effective as exposure with contact? Rasa (1971) explored these questions in a preliminary way. She determined, for instance, that a moving inanimate stimulus did not substitute for a rival fish in reducing the effects of deprivation and thereby ruled out a decrease of stimulation in general as an explanation for her results. In

addition, she concluded that the effects of deprivation were not entirely explained by an increase of activity in general, although changes in activities other than clear aggression occurred after deprivation. In these first attempts to determine the specificity of the stimulus and the effects of deprivation, Rasa included no investigation of nonaggressive interactions with conspecifics.

When the opponent's previous social experience is manipulated, in addition to the subject's, the behavior of isolated male mice and gerbils depends on the treatment of the opponent. Isolated animals tested with animals from groups often do not fight. Isolated male gerbils are more likely to investigate their partners during tests in a new environment, while males with continuous social experience investigate objects rather than their partner in the test (Spencer *et al.*, 1973). This difference in the orientation of exploratory behavior leads to more frequent fights when isolates are tested together than when isolates are tested with nonisolates or when nonisolates are tested together. The predominant orientation of isolated animals to their partners in tests perhaps explains why isolated mice are not more dominant or more likely to initiate aggression when tested in their own, as opposed to the partner's, home cage (Banerjee, 1971).

A related effect of previous experience might also influence spacing: a history of defeats or wins in dyadic encounters results in tonic suppression or facilitation of aggression toward strangers (Collias, 1943; Scott and Fredericson, 1951; Lagerpetz, 1961). This effect probably has little influence on spacing behavior in natural populations, where individuals usually withdraw from encounters before serious defeat and, by moving to new areas, can avoid long histories of defeat. Within cohesive groups, in contrast, suppressed aggression following repeated losses probably has important effects on the structure of agonistic behavior. Spacing is perhaps most directly affected by this mechanism when some individuals remain as subordinates associated with territorial individuals rather than establishing their own exclusive areas, as do male white rhinoceros (*Ceratotherium simum*) (Owen-Smith, 1972, 1975).

When rates of social interaction with opponents have tonic effects on an individual's agonistic tendencies, these effects tend to damp any changes in spacing in response to transient changes in population pressure. Morse (1976) found that the sizes of warblers' (*Parulidae*) territories changed less rapidly than did population density over a period of several years, an indication that such inertia in spacing behavior occurs in the field. Tonic increases in individuals' aggressive tendencies in sparse populations would counteract abrupt changes in spacing in response to changes in the numbers of individuals seeking to establish themselves.

Experiments on the effects of previous experience on aggression have generally not attempted to elucidate the control of spacing in natural circumstances. Studies should consider (1) a greater range of the subjects' responses, including avoidance; (2) different kinds of stimulation from social interactions; and (3) different rates of exposure to social stimulation. Conclusions about the effects of different rates and kinds of social interaction on aggressiveness would have direct relevance to an understanding of individual and population differences in spacing in natural circumstances.

**EFFECTS OF FOOD AVAILABILITY.** In some species, territory sizes in different habitats correlate with the densities of available food in these habitats (see Schoener, 1968b). Stenger (1958) has come close to a direct demonstration of this relationship by sampling insect densities in the leaf litter of different habitats of ovenbirds (*Seiurus aurocapillus*). In red grouse (*Lagopus lagopus*), differences in territory sizes among populations correlate with the nutrient content of growing heather, the principal food of the adult grouse (Miller, Jenkins, and Watson, 1966; Miller, Watson, and Jenkins, 1970; Moss, 1969). Year-to-year changes in territory densities of any one grouse population are also correlated with changes in heather quality but with a one-year lag in the response. Indirect evidence suggests that differences in territory size among populations of other species might also correlate with densities of available food. Moreover, individuals of some species, like the white wagtail (*Motacilla alba*) in winter, switch from a relatively unaggressive state to vigorous defense of small territories in the presence of concentrated food sources (Zahavi, 1971). In some nectar-feeding birds, aggressive interactions decrease at high food densities when food becomes superabundant (Gill and Wolf, 1975a; Carpenter and MacMillen, 1976b). However, food densities do not always regulate agonistic tendencies, since seasonal changes in territorial behavior in some bird populations are not synchronized with seasonal changes in food availability or dispersion (see Watson and Moss, 1970).

If individuals adjust their spacing to the available food, their tendencies to avoid, threaten, approach, and attack conspecifics at different locations or separations must change when food supplies change. These adjustments do not require direct responses to the ease or frequency of finding food or to the individual's hunger, but such responses would provide a mechanism for regulating spatial relationships in relation to food availability.

Experimental studies have explored the effects of acute food deprivation on the frequency of aggression between individuals in small groups. Such studies and anecdotal reports of field observations usually provide evidence that rates of aggression increase with hunger. However, according to more careful analyses of interactions in small flocks of finches and buntings, hunger increases the frequency of close approaches between individuals by reducing individuals' tendencies to avoid more dominant individuals, so that circumstances provoking threat and attack occur more frequently, yet the probability of attacks from a given separation remains unchanged (Marler, 1956b; Andrew, 1956). Rohles and Wilson (1974) have similarly shown that food deprivation increases the frequency of aggression among laboratory mice by increasing the frequency of close approach.

The effects of chronic hunger might differ from those of acute deprivation. Field studies of a North American bunting (*Junco hyemalis*) suggest that hunger, as a result of low temperatures during winter, reduces the frequency of aggression at localized food sources (Sabine, 1959; Pulliam, 1974). Pulliam's observations show that during colder weather, frequencies of threat and attack decrease for any separation of individuals. Sabine suggested that dominant individuals in these circumstances become habituated to the persistent, close approaches of subordinates. These field studies thus indicate that hunger reduces aggressive tendencies

for any specified separation of opponents, although temperature might directly affect activity. The changes in agonistic behavior of sunbirds and wagtails around concentrated food sources (see above) also suggest that in some circumstances a full stomach, rather than hunger, can encourage sedentariness and aggression.

**AGONISTIC INTERACTIONS AND INDIVIDUAL DIFFERENCES IN TERRITORY SIZE.** Within a population, individuals often differ in the sizes of their territories, and these differences are often thought to reflect individuals' differences in aggressiveness. Attempts to relate territory size to the resident's agonistic behavior, however, indicate that this relationship is complex.

Among red grouse in Scotland, territory size within one population correlated with an index of aggression based on both the frequency and the outcome of a resident's agonistic interactions (Watson and Miller, 1971). Although these authors inferred that greater aggression causes the larger territories, this causality is not certainly established. If larger territories had more frequent intruders, residents would engage in more frequent agonistic interactions. If intruders normally withdrew, holders of large territories would also have more frequent interactions in which the opponent withdrew. The greater index of aggression might thus result from, rather than cause, the larger territories. Since males implanted with testosterone enlarge their territories (Watson, 1970), a resident's aggressiveness clearly influences territory size, at least when neighbor's tendencies are not manipulated. In natural circumstances, territory size is likely to result from an interaction of the resident's and the neighbors' tendencies. Available evidence, however, does not establish the nature of this interaction. The finding that the sizes of territories in any one area and year correlate with the quality of food they contain (Lance, 1978b) suggests either that males adjust their aggressiveness in inverse relation to the quality of available food (Watson and Moss, 1972) or that competition for territories is greater in locations with better food. Variation in territory size from year to year also admits of alternate explanations. When breeding success is high, more young males subsequently establish territories, these territories are smaller, and aggression is lower than when breeding success is low (Watson and Miller, 1971). This situation could result from differences in the intrinsic aggressiveness of males reared in good and bad years (Watson and Moss, 1972) or from differences in the intensity of competition for territories in accordance with the numbers of young males reared. To establish the relative effects of residents' and neighbors' tendencies in the determination of territory sizes, it would help to study the responses of territorial males to standard stimuli.

To investigate the probability and intensity of attack or threat by an individual toward a standard opponent in a controlled location, Spurr (1974) presented realistic models to territorial Adélie penguins (*Pygoscelis adeliae*) in a dense nesting colony. Individuals with high rates of pecking tended to have more central locations in the colony and higher breeding success than did individuals with lower rates of pecking. The central location of the more aggressive individuals is probably only partly caused by their aggressiveness, as the older central individuals tend to return to the nesting area before the younger, peripheral penguins. Thus, younger individuals occupy larger territories in less desirable areas, and

although they have lower aggressive tendencies in an experimental situation, they encounter more intruders and engage in more frequent agonistic encounters.

When neighboring territories differ in their attractiveness for residents, territory sizes are determined as much by neighbors' tendencies as by the residents'. On leks of sage grouse (*Centrocercus urophasianus*), where most copulations occur at the center of an aggregation of males' territories, a male spends most of its time on the side of its territory nearest this mating center. Among pairs of neighbors with territories along a radius from the center, the more central individual initiates most boundary interactions by dashing across his territory, from his preferred place closest to the center, to confront his neighbor encroaching centripetally. Consequently, residents initiate most of their encounters with more peripheral neighbors and parry the challenges received from their more central neighbors (Wiley, 1973). The central territories are smaller, presumably owing both to the greater preoccupation of the residents with females and the greater pressure of more peripheral neighbors toward the mating center. The behavioral regulation of an individual's isolation field in these sage grouse, as in red grouse and penguins, most likely depends on the external pressure from intruders as well as on the internal resistance from the resident.

#### CATEGORIES OF INDIVIDUALS THAT ENGAGE IN SPACING BEHAVIOR

**DIFFERENTIATION OF THE SEXES.** In species as diverse as weasels (*Mustela* species) (Lockie, 1966), parrotfish (*Scarus croicensis*) (Buckman and Ogden, 1973), and dragonflies, *Odonata* (Campanella and Wolf, 1974), the sexes differ in their spacing behavior. In polygamous species of both birds and mammals, aggression between members of the limiting sex is reportedly infrequent. In many polygynous ungulates, females are gregarious while males tend to be solitary and mutually aggressive (Jarman, 1974; Geist and Walther, 1974). Among tenrecs, prosimians, and other "solitary" mammals, females' home ranges often overlap more than do males' (Charles-Dominique, 1974; Eisenberg, 1975, 1977). In most monkey species, males play the primary role in intergroup conflicts (Clutton-Brock and Harvey, 1976). When both sexes are involved in spacing interactions, aggression is generally intrasexual; in the red-winged blackbird, females have been reported to defend small territories among themselves within the larger territories of a male (Nero, 1956).

Among monogamous species, females vary from showing almost no participation in territorial defense to participating as extensively as males. In the American robin (*Turdus migratorius*), a monogamous species with extensive territories, quantitative information is available on agonistic behavior of both sexes (Young, 1951). The activity fields of neighboring pairs overlap extensively in this species, although the areas used most intensively by each pair (core areas) overlap much less. Both sexes are more likely to engage in intrasexual than intersexual interactions. Females have greater success in both intra- and intersexual interactions within their own core areas than outside them, but location seems not to influence the success of males.

TABLE II. SOME EXAMPLES OF SEXUAL ROLES IN TERRITORIAL DEFENSE AMONG  
MONOGAMOUS PASSERINE BIRDS

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A. Both Sexes Regularly Defend Territory against Intruders

1. Species with sexually monomorphic plumage; territorial defense both intra- and intersexual
  - Wheatear *Oenanthe oenanthe*  
(Conder, 1956)
  - Wrenit *Chamaea fasciata*  
(Erickson, 1938)
  - Black-capped chickadee *Parus atricapillus*  
(Stefanski, 1967)
  - European robin *Erithacus rubecula*  
(Lack, 1943)
2. Species with sexually dimorphic plumage; territorial defense intrasexual only
  - American redstart *Setophaga ruticilla*  
(Ficken, 1962)
  - Galapagos finches, Geospizinae<sup>a</sup>  
(Lack, 1954)
  - Chaffinch *Fringilla coelebs*  
(Marler, 1956a)
  - Snow bunting *Plectrophenax nivalis*  
(Tinbergen, 1939)
  - American robin *Turdus migratorius*<sup>b</sup>  
(Young, 1951)

B. Male Only Defends Territory against Intruders; Territorial Defense Both Intra- and Intersexual

- House wren *Troglodytes aedon*  
(Kendeigh, 1941)
- Ovenbird *Seiurus auricapillus*  
(Stenger and Falls, 1959)
- Great tit *Parus major*  
(Hinde, 1952)
- Meadowlarks *Sturnella magna*, *S. neglecta*  
(Lanyon, 1957)
- Song sparrow *Melospiza melodia*<sup>c</sup>  
(Nice, 1943)

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<sup>a</sup>Males defend territories against intruders of both sexes, females only against other females.

<sup>b</sup>Species with weakly developed dimorphism in plumage; territorial defense primarily but not exclusively intrasexual (see text).

<sup>c</sup>Defense primarily intrasexual.

Though quantitative data for other avian species are lacking, the degree to which females regularly confront intruding individuals appears to correlate with sexual dimorphism (Table II). In monogamous dimorphic species, females are normally involved in territorial defense, but, as in American robins, they normally engage only other females. In some monogamous, monomorphic species, like the European robin (*Erithacus rubecula*), both sexes regularly defend the territory; in others, like the meadowlarks (*Sturnella* species), only males do so. In both cases, however, defense is inter- as well as intrasexual.

Among mammals, spacing is commonly intrasexual, and male and female activity fields are often not congruent. In many carnivores, especially Felidae and Mustelidae, males have large, mutually exclusive ranges that overlap the smaller ranges of females (Lockie, 1966; Erlinge, 1968; Hornocker, 1969; Muckenhirn and Eisenberg, 1973; Kleiman and Eisenberg, 1973).

Among dikdiks (*Madoqua kirki*), elephant shrews (*Elephantulus rufescens* and

*Rhyncocyon chrysopygus*), and red fox (*Vulpes vulpes*), male and female home ranges become completely overlapping, so that mating occurs exclusively within pairs even though individuals are only occasionally associated spatially (Hendrichs and Hendrichs, 1971; Kleiman, 1977; Rathbun, in press). Among dikdiks, males defend largely exclusive territories against intruders of both sexes (Hendrichs and Hendrichs, 1971).

On the other hand, mammals with strong tendencies for long-term heterosexual associations combine monogamous bonds with sex-specific aggression. Among certain species of gibbon (*Hylobates*), marmoset (*Callithrix*), titi monkey (*Callicebus*), and jackals (*Canis*), members of a pair are nearly always found together, and aggression between pairs is primarily intrasexual (Chivers *et al.*, 1975; Epple, 1975; Kleiman, 1977; Moehlman, 1977; Robinson, in press; Tenaza, 1975)—a situation resembling that among monogamous, dimorphic birds.

Even among monogamous animals, mates' activity fields are not always congruent. In some species, mates never achieve a close match in the limits of their activity fields. Kendeigh (1941) reported that female house wrens (*Troglodytes aedon*) persistently venture beyond their mates' boundaries in spite of regular eviction by the neighboring males. In contrast, female tree sparrows have substantially smaller activity fields than males (Weeden, 1965).

Observers often note that females seem unaware of their mates' boundaries at first but that their activity fields eventually become more similar. Congruence between the activity fields of mates requires either (1) that one match its activity field to the other's by direct experience with its movements independent of agonistic interactions with neighbors or (2) that each develop corresponding relationships between its movements and agonistic interactions with neighbors. As reviewed previously, males sometimes modify their activity and aggression fields when their mates select nest sites near or beyond their previous territorial borders. These males appear to adjust their spacing behavior as a result of direct experience with their mate's movements. Agonistic interactions with neighbors, on the other hand, seem likely to influence the movements of females as well as males. Among some birds that are monomorphic in plumage, females maintain individual territories during the winter but join a male on his territory for breeding (Lack, 1943; Miller, 1931; Michener and Michener, 1935). During the process of pairing, when the female shifts her activity and aggression fields to coincide with those of her mate, both sexes defend the pair's territory against intruders. Similar trends have been found among monogamous mammals, for instance, gibbons (Tenaza, 1975) and some carnivores (Kleiman and Eisenberg, 1973). These considerations suggest that congruent activity fields of mates in monogamous species often require agonistic interactions of both males and females with neighbors, rather than adjustment of one member's activity field to the other's through direct experience with others' movements.

**OTHER CATEGORIES OF OPPONENTS.** An individual's agonistic behavior varies with attributes of an opponent other than its sex, particularly special behavior of the opponent and the opponent's familiarity. Field studies and some laboratory studies suggest that the probability or intensity of an individual's aggressive behavior often depends on the opponent's behavior. Early descriptions of territo-

rial behavior in birds noted that intruding individuals often evoke the resident's aggression only after they sing (Tinbergen, 1939; Lack, 1943), and subsequent field studies have often reported similar observations. The European robin's red breast, the male chaffinch's orange underparts, and the orange opercular patch of male cichlids (*Haplochromis burtoni*) increase the aggression evoked from other individuals (Lack, 1943; Marler, 1955b, 1956b; Heiligenberg, 1965; Leong, 1969). Among fish, coloration can change within seconds, so that a trespassing individual can adopt alternative color patterns quickly. In *Haplochromis*, a male that retains its nonterritorial coloration would escape much of a territorial resident's aggression even when detected. Among certain amphibians, birds, and mammals, specific behavior patterns of certain males allow them to coinhabit territorial males' activity fields. Cessation of calling and adoption of the "low" posture allows "satellite" male bullfrogs (*Rana catesbeiana*) to remain within a few meters of calling males (Emlen, 1976). Ovenbirds tethered to the forest floor do not sing and are not attacked by the territory owner (Zach and Falls, in press). Tolerance by male white rhinos of other "nonterritorial" males is associated with their abandonment of spray-urination and dung-scattering behavior (Owen-Smith, 1975). Do transitory advertising displays, such as singing or scent marking, increase a resident's aggressive tendencies toward the signaler, or do they only increase the probability of detection?

Opponents' familiarity with each other usually decreases aggression. In studies of macaques, hens, rats, and mice, in which prior familiarity with an opponent reduced aggression, the establishment of familiarity included the establishment of a polarized, dominance-subordination relationship (e.g., Craig, Biswas, and Guhl, 1969; Southwick, Farooqui, Siddiqi, and Pal, 1974). During reunion after a period of separation, this relationship was evidently remembered and went unchallenged. In experiments with bobwhite quail (*Colinus virginianus*), a reduction in aggression as a result of prior exposure to opponents did not even require that the initial exposure include physical contact (Garreffa, 1969). Relatively solitary species often fight bitterly without cessation when individuals are confined together (e.g., Lorenz, 1952). In natural circumstances, however, even solitary mammals become less aggressive toward each other with familiarity. Raccoons (*Procyon lotor*) and foxes (*Vulpes fulva*) engage in less aggression when conspecifics trapped at localities near each other are confined together than when conspecifics from more widely separated localities are paired (Barash, 1974).

Among territorial birds and fish, agonistic interactions between neighbors wane in frequency and intensity after territory establishment. Studies of convict cichlids (*Cichlasoma nigrofasciatum*) and three-spined sticklebacks (*Gasterosteus aculeatus*) have demonstrated the similarity between this phenomenon and other forms of habituation (Peeke, Herz, and Gallagher, 1971; van den Assem and van der Molen, 1969). Perhaps the most striking demonstrations of waning responses to neighbors have employed playbacks of advertising song to territorial passerines. Such experiments have shown that a wide variety of species respond much less reliably and intensely to playbacks of neighbors' songs than to strangers' songs. This difference apparently results in part from habituation of territorial residents' responses to advertising vocalizations heard regularly. Several studies have documented waning responses to repeated playbacks of advertising songs (Verner and



Milligan, 1971; Brooks and Falls, 1975); territorial male white-throated sparrows (*Zonotrichia albicollis*) respond more intensely to playbacks of neighbors' songs early in the season than later, while responses to playbacks of strangers' songs do not decrease (Brooks and Falls, 1975). On the other hand, a recent study of towhees (*Pipilo erythrophthalmus*) with abnormal songs demonstrated that neighbor-stranger discrimination can result from associative learning rather than habituation to familiar songs (Richards, in press).

Of special significance for the control of spacing are cases in which recognition of neighbors' vocalizations is specific to the usual direction from which the neighbor sings. This feature of neighbors' interactions has so far been demonstrated only for two species of passerines: white-throated sparrows, a species that establishes individual territories, and stripe-backed wrens (*Campylorhynchus nuchalis*), which maintain group territories and perform duets and choruses as advertising vocalizations (Falls and Brooks, 1975; Wiley and Wiley, 1977). At least in the latter species, residents do not attend to the differences between neighbors' vocalizations in the correct and the wrong places as promptly as they do to the differences between neighbors' and strangers' vocalizations. If neighbors rarely sang from outside their own territories, an ability to recognize neighbors out of place promptly would confer little selective advantage. Individual recognition of opponents and association of each with its usual locations are especially important when individuals' ranges overlap substantially.

## CONCLUSION

Our review of the behavioral mechanisms of spacing began by emphasizing the importance of site-dependent agonistic behavior. Although changes in agonistic tendencies in accordance with the proximity of opponents influence the simultaneous locations of individuals, site-dependent agonistic behavior can more reliably generate evenly distributed activity fields. Yet, ethology so far has little clear evidence about the behavioral mechanisms that generate spatial variation in tendencies to approach, avoid, or attack opponents. A similar lack of precision or interest has also hampered our understanding of the behavioral mechanisms that produce individual and population differences in spacing behavior or the mechanisms that control spatial relationships of the sexes. The time seems ripe for a full integration of laboratory and field experimentation on aggression and spacing.

## COMMUNICATION OF ADVERTISEMENT OR THREAT

Analysis of spacing mechanisms is complicated by the existence of advertising behavior that influences the movements of a conspecific at locations or times removed from the performance of the behavior. Clearly, if an organism can elicit avoidance by its neighbors by means of a long-range or persistent signal rather than a physical contest, it stands to reduce both its risk of injury and its expenditure of energy by doing so. Because conspicuousness is an expected characteristic of such signals, it is not surprising that "distance-increasing" behaviors (Marler, 1968) have been widely described. They range from the urination of mice and the

dung-piling of rhinoceroses to the bright colors of reef fish and the vocal choruses of bullfrogs, songbirds, and forest primates.

#### GENERAL CONSIDERATIONS

Spacing signals can modify the relationships between activity, aggression, and isolation fields in a number of ways. For instance, signals influence the distance and the locations at which neighbors detect each other and thus the degree to which they may penetrate each other's ranges without a face-to-face encounter. Perhaps even more important is the influence of signals on the means by which aggression fields regulate spatial relationships. Agonistic tendencies underlying overdispersed activity fields might emphasize either avoidance or aggression; overdispersion could result either from aggressive reactions to stealthy opponents or from avoidance of advertising signals. On the continuum between aggression and advertisement, on the one hand, and stealth and avoidance, on the other, species have struck different balances.

Environmental factors that alter neighbors' probabilities of detecting each other can have pronounced effects on their isolation fields. In laboratory situations, partial physical barriers within an enclosure sometimes allow two individuals to establish areas of dominance where only one becomes established in the absence of barriers (Sale, 1972; Jenni, 1972). Habitats with dense vegetation might have similar effects (Burger and Beer, 1975). By reducing movements, barriers might limit individuals' activity fields even in the absence of opponents and thus make it easier for a second individual to establish itself. In addition, the obstruction of communication by the barriers reduces the frequency of encounters across the barrier and consequently might permit the establishment of two individuals at closer spacing.

The costs as well as the efficacy of spacing signals vary between species. Perched hummingbirds (*Eulampis jugularis*) broadcast a continuous visual spacing signal at little caloric cost (Wolf and Hainsworth, 1971). When male black-and-white colobus bask in the sun in emergent trees, their conspicuous coat may even provide a net energy gain (Oates, 1976). Olfactory spacing signals used by mammals frequently involve the metabolic by-products sometimes produced by commensal bacteria (Gorman, Nedwell, and Smith, 1974). On the other hand, in singing katydids, metabolism can increase by an order of magnitude over resting rates (Stevens and Josephson, 1977). Even when the broadcasting of a spacing signal is energetically cheap, any conspicuous signal potentially carries an increased risk of predation. The magnitude of such risks remains to be investigated, but their presence suggests that the use of long-range signals should not be universal.

The possibility of substituting threats or long-distance signals for overt attacks also introduces two new behavioral alternatives not otherwise open to the contestants: bluffing, in essence suggesting a greater likelihood of detecting or evicting an intruder than actually exists; and calling bluffs, by ignoring spacing signals and attempting to avoid detection (Maynard Smith and Price, 1973; Parker, 1974; Maynard Smith and Parker, 1976). Consider a long-distance spacing call: it is

advantageous for the sender to increase its range as long as this increases the area from which neighbors are excluded. But neighbors hearing the call can also use it to determine into which areas intrusion is unlikely to be detected, a possibility that increases with distance from the sender. How accurately, and over what distance, should an individual broadcast its location?

#### CHANNELS FOR SPACING SIGNALS

Presumed spacing signals have employed all sensory modalities, even electrical (Hopkins, 1974). For long-range transmission, the modalities of choice are usually auditory and olfactory: the former where separation of individuals in space at any one time is of primary importance; the latter especially for separation in time of activities at any one place. The channel of choice thus depends in part on the spatial and temporal distribution of the resources at issue and on their renewal rates.

The optimal modality for spacing communication also varies with the amount of interference in the available communication channels. Many forest primates, from lemurs to apes, possess long-range vocalizations with presumed spacing functions, whereas these have not been described in patas monkeys, baboons, geladas, or other primates of open country, where long-range visual communication is possible. The forest-living, nocturnal tree hyrax broadcasts its location several times nightly with deafening, long-distance screams, while the diurnal rock hyraxes have no comparable vocalizations. Reef fish in clear shallow water are brightly colored and possess conspicuous visual displays; fish in deeper or more turbid waters are more likely to be drab but acoustically or electrically conspicuous. Constraints placed by various environments on visual signals are at least qualitatively obvious to us; comparable acoustic and olfactory constraints are much less well known.

The size of the area within which exclusion of competitors is worthwhile could also influence the choice of a modality. Considering that smaller animals usually maintain smaller mean interindividual distances, one might expect a general trend toward visual signals in smaller animals, auditory or olfactory in larger ones. Exaggerated visual-spacing displays are most common in small, closely spaced diurnal animals such as lizards, coral reef fish, and intertidal crabs, while elaborate olfactory marks or acoustic signals characterize larger, mobile mammals and birds.

Finally, the modalities differ in the precision with which the sender can be located. Visual signals completely specify the current location of the signal source; acoustic and olfactory signals may not. When the interests of sender and receiver are opposed, as in the long-distance spacing call discussed above, this characteristic may also affect the sender's choice of modality.

The formulation of specific hypotheses concerning the expected modality of spacing signals is only beginning. One approach to the problem, the computer simulation of animal movements and interactions, has been initiated by Montgomery (1974). Taking distributions of rates of movement and rates of turn from radio-tracking data, Montgomery determined the potential frequencies of contact between individual foxes on the same home range that would result from a variety

of hypothetical visual, auditory, and olfactory signals. Simulation models could readily be extended to investigate efficiencies of communication between individuals in adjacent ranges.

#### ADAPTATIONS OF SIGNAL STRUCTURE

The range of many acoustic spacing signals is impressively long: the drumming of ruffed grouse (*Bonasa umbellus*) (Archibald, 1974); the roar of lions (*Panthera leo*) (Schaller, 1972); and the loud calls of many forest primates (Altmann, 1967; Marler, 1968). Sound propagation in different vegetation types has been investigated with a view toward understanding the evolution of signal form (Chappuis, 1971; Morton, 1975; Marten, Quine, and Marler, 1977; Marten and Marler, 1977) for long-range communication. In both West African (Chappuis, 1971) and Central American (Morton, 1975) forests, there is at least a general tendency for the dominant frequencies of avian songs to match frequency bands with superior transmission characteristics and for tonal signals to replace the complex spectra or rapid frequency modulations characteristic of avian songs in open habitats.

The hypothesis that spacing calls are specialized for long-distance transmission has been directly investigated only for some forest primates. Audible range is influenced by source sound levels, background noise levels, rates of signal degradation, and the perceptual abilities of the receiver. Waser and Waser (1977) have investigated the first three parameters for primate species in a Ugandan rain forest. Relative to other calls in their vocal repertoires, the long-distance vocalizations of *Colobus guereza*, *Cercopithecus mitis*, *C. ascanius*, and *Cercocebus albigena* show significantly lower rates of attenuation when broadcast and rerecorded after passage through the forest canopy. Transmission experiments using pure tones suggest that the spectral distribution of energy in these calls is a primary factor responsible for their decreased attenuation rates; temporary transmission "windows" at intermediate frequencies (500–2000 Hz), as well as efficient transmission at low frequencies (125 Hz), were characteristic of the forest canopy. Long-distance calls were also found to have less variable attenuation rates than either nonspacing calls or pure tones. Evidently, aspects of signal structure other than modal frequency are of importance in their transmission. Sound propagation experiments carried out at different heights and times of day also indicated that calling from heights of 15–20 m (normal for a monkey) can more than double the audible range of the call over that at 1.5 m, and that primate species tend to concentrate their long-distance vocalizing either before dawn, when background noise was found to be lowest, or in early morning, when attenuation rates for those calls dropped by several db/100 m.

In contrast to their specialization of form and timing, the long-distance vocalizations of these primates were not characterized by unusually high sound levels at the source; frequently these did not exceed the levels of other calls in the repertoire. Moreover, sound levels of long-distance primate calls are equaled by those produced by much smaller animals, including cicadas and Orthoptera (Dumortier, 1963), frogs (Gerhardt, 1975), and birds (Morton, 1975). One possible expla-

nation for this phenomenon lies in the physical nature of sound attenuation. Attenuation losses from spherical spreading of energy from a point source—losses that can generally be overcome only by an increase in source sound level—fall off logarithmically with distance, roughly 6 db for each doubling of distance from the source. On the other hand, losses from sound absorption—which can be reduced by modifying signal structure—are related to distance in an approximately linear fashion. As distance from the source increases, absorption accounts for an increasing proportion of the total attenuation.

Long-distance transmission of acoustic signals near the ground is affected by interference from sound reflected by the ground. This ground attenuation, confirmed repeatedly in transmission experiments with pure tones (Marten and Marler, 1977; Marten *et al.*, 1977; reviewed by Wiley and Richards, 1978), depends on the height of the source and the receiver in relation to the wavelength of the sound and on the acoustic impedance of the ground, which in turn varies with features of the soil and the ground vegetation. As the height of the transmission path above the ground increases, the wavelength for maximum ground attenuation also increases (see Wiley and Richards, 1978). For transmission within a few meters of the ground, a well-marked transmission “window” occurs for intermediate frequencies (1–3 kHz) (Morton, 1975; Marten and Marler, 1977; Marten *et al.*, 1977); lower frequencies are subject to greater attenuation from ground reflection, higher ones to greater attenuation from atmospheric absorption and scattering. In addition, reverberation in forests is minimal between 1 and 3 kHz (Richards and Wiley, *in press*). Most territorial birds in forests use this frequency band for their long-range acoustic signals (Morton, 1975; Richards and Wiley, *in press*).

Sound transmission in natural habitats has other properties, in addition to frequency-dependent attenuation, that affect the evolution of signal structure. Rapid variations in background noise, reverberation, and random fluctuations in amplitude from turbulence (Knudsen, 1946; Ingard, 1953; Wiener and Keast, 1959; Marten and Marler, 1977; Richards and Wiley, *in press*; Waser, personal observation) limit the use of intensity patterns and rapid, repetitive frequency patterns for long-range transmission of information (Wiley, 1976b; Wiley and Richards, 1978). Greater reverberation in forests, in comparison to open habitats, probably explains why many forest-dwelling birds avoid rapid repetitive frequency modulation in their advertising songs (Chappuis, 1971; Morton, 1975; Richards and Wiley, *in press*).

A vocalizer also faces different problems in communicating his direction and distance in different habitats. Mangabeys are able to localize single experimentally broadcast spacing calls with a median accuracy of 6° from a distance of several hundred meters (Waser, 1977b), despite the fact that many of the classical cues for direction (Konishi, 1973) are greatly degraded at that distance. High frequencies have been differentially attenuated, and scattering has blurred sharp onsets. Of course, these types of degradation also provide a listener with information on source distance (Griffin and Hopkins, 1974; Coleman, 1963; Wiley and Richards, 1978).

The constraints operating on spacing signals in other sensory modalities are

much less well understood. Background noise from distant lightning, as well as rapid signal attenuation, is a constraint on the electrical signals used by some tropical fish (Hopkins, 1974). Olfactory signals have two characteristics of obvious relevance to their use in spacing: fade-out time and active space. The flank marks of male golden hamsters (*Mesocricetus auratus*) elicited responses for 25–50 days after their deposition, the first measurement of fade-out time for presumptive olfactory spacing signals (Johnston and Lee, 1976). Fade out time and active space vary with rate or frequency of deposition, sensitivity of receptors, and rates of diffusion of the chemical signal (Bossert and Wilson, 1963; Wilson and Regnier, 1971). Rate of odorant release depends not only on such chemical properties of the signal as molecular weight and functional groups but also on environmental factors such as adsorptivity of substrate, ambient humidity, and local wind speed. The fade-out time of a nonpolar molecule can also depend on whether or not it is deposited in conjunction with a lipid (Regnier and Goodwin, 1977). The deposition of a fixed proportion of both polar and nonpolar molecules in a lipid (or any other combination of molecules with different diffusion rates) allows detection of the age of an olfactory mark.

Although adaptations for communication between individuals in the end determine the possibilities for spacing without close-range encounters, studies of the properties of signals that permit the transmission of information to long distances or over long time periods have just begun.

## EVOLUTION OF SPACING BEHAVIOR

Regardless of the behavioral mechanisms of spacing, natural selection should adjust these mechanisms to maximize the propagation of individuals' genes. For over a quarter of a century after Howard's (1920) seminal treatment of territoriality, discussions of the evolution of spacing centered on the "functions" of territoriality: the importance of this behavior for securing a reserve of food, for isolation from interference in pair formation, and for protection from predators or epidemics (reviewed by Hinde, 1956). This discussion revolved in part around the distribution of various activities with respect to an individual's defended area. Few firm conclusions could be reached, in part because of the variety of relationships among feeding, pair formation, and territories in different species or even different populations of the same species. In retrospect, much of this literature suffers from the allied shortcomings of failing to analyze in detail the variable spatial relationships of individuals' activities and agonistic tendencies and seeking to explain the evolution of territoriality as a unitary phenomenon, rather than attempting to identify differences in selection pressures that might explain variations in activity, isolation, and aggression fields.

The appearance of Wynne-Edwards's book (1962) changed the emphasis in studies of territoriality. He contended that territorial behavior, and indeed many forms of social behavior, had the effect of limiting population densities and evolved because of the adaptedness of limitations on density that would prevent excessive exploitation of food resources. In contrast, Lack has long argued that

territorial behavior does not limit population densities but only disperses individuals once settled (Lack and Lack, 1933; Lack, 1966) and that, in general, populations, whether territorial or not, are limited directly by the food available.

There are several differences between Lack's and Wynne-Edwards's positions. To begin with, they differ with regard to the behavioral mechanisms of territoriality. Two questions are pertinent here. First, to what extent do territorial individuals exclude newcomers? Second, do the behavioral mechanisms of territoriality permit adjustments to immediate or recent experience with the food supply? As has been discussed in the second section, the relationships of activity fields and agonistic behavior to isolation fields differ among species, so that neither Lack's nor Wynne-Edwards's view permits unqualified generalization.

Lack's and Wynne-Edwards's positions also differ on evolutionary questions: How important is competition between demes in the evolution of the larger population's gene pool? Can any selection regime favor the evolution of behavior that limits population density below maximum exploitation of resources? The first question has received thorough debate. The consensus agrees with Lack in minimizing the importance of interdemic selection (Williams, 1966, 1971; Maynard Smith, 1958; see Wilson, 1975, for a review of recent literature). The latter question hinges on the proper balance of short- and long-term advantages in the evolution of density-dependent reproduction. We are not aware of any formal treatment of this problem.

In retrospect, both Lack and Wynne-Edwards seem to have overlooked significant variations in spacing behavior among species and consequently proposed oversimplified explanations for the evolution of spacing mechanisms.

#### COSTS AND BENEFITS OF SPACING

The evolutionary advantages of spacing behavior, most of them enumerated early in the study of territoriality, are probably never without qualifications. Both wide dispersion and aggregation confer conflicting advantages and disadvantages. Thus, predators are in some cases more reliably detected or repelled by groups of individuals, yet groups more often catch a predator's attention. Aggregation can have advantages for individuals in finding or capturing food (Krebs, this volume), yet aggregation increases the demands on locally available resources.

Spacing behavior, like most social interaction, takes time and energy and involves some risk of injury or exposure to predators. The advantages of the social relationship achieved by these interactions must thus compensate the participants for the costs of the interactions. Brown (1964) and Brown and Orians (1970) introduced such an economic analysis of the costs and benefits to individuals in terms of changes in their fitnesses, or the rates of propagation of their genes.

The evolution of territorial defense, as Brown indicated, requires that the individual obtain some benefit as a result of increased access to a limiting resource and that the costs of defense be less than the benefits. Because cost and benefit are decreases or increases in the fitnesses of genes associated with the expression of territorial defense, a resource is limiting if its availability influences an individual's survival or reproduction. Brown's formulation suggests particular questions about

the evolution of spacing. What, for any given population of animals, are the limiting resources? And what, in general terms, are the attributes of a resource that make it defensible?

Because ephemeral aggregations of food are difficult to defend, many seabirds that feed on schools of fish and swallows that locate aggregations of flying insects nest in colonies and do not defend territories. Conversely, territorial defense occurs in many animals that feed on relatively evenly dispersed and temporally stable populations of prey, such as birds taking insects on foliage or monkeys feeding on leaves (see Crook, 1961; Eisenberg, Muckenhirn, and Rudran, 1972). Larger areas become more difficult to defend, and animals requiring them, like patas monkeys (*Erythrocebus patas*) in open savanna and nomadic ungulates, often lack elaborate spacing behavior (Hall, 1965; Jarman, 1974). Beyond these gross generalizations, the "defensibility" of resources is related to the availability, spatiotemporal dispersion, and turnover rates of resources in complex and as yet poorly understood ways. Schoener (1971) has developed a formal expression of the net benefit of territorial defense as a function of the area defended and the effectiveness of defense, but we still lack a model with sufficiently few and accessible parameters to allow reliable predictions for most species in the field.

Despite these difficulties, the territorial behavior of certain nectarivorous birds is predicted remarkably well by cost-benefit analyses (Wolf and Hainsworth, 1971; Gill and Wolf, 1975a,b; Carpenter and MacMillen, 1976a,b). For some hummingbirds, sunbirds, and depreanid honeycreepers, one can measure the amount of food in a territory and its rate of production by determining the density of flowers, their nectar content, and their rates of nectar production. Individuals defend feeding territories when the metabolic costs of defense are compensated by a gain in nectar availability (Gill and Wolf, 1975b; Carpenter and MacMillen, 1976b). In particular, territoriality occurs neither when food densities are very low, so that the gain in available food (in calories) does not compensate the costs of defense (in calories), nor when food densities are very high, so that the presence of competitors has little effect on available food. In addition, increased numbers of competitors raise the costs of defense and can result in abandonment of territoriality (Stiles and Wolf, 1970). In species like nectarivores, for which food occurs in patches that vary markedly in richness across time and locations, individuals change from nonterritorial to territorial behavior in accordance with food availability in defended and undefended areas and the intensity of competition for rich sites.

An inherent difficulty with cost-benefit analyses is that the behavior of intruders, as well as residents, is likely to depend on the distribution and abundance of a limiting resource. Because properties of the resource that make it beneficial for a resident are likely to make it attractive for an intruder, the benefits and the costs of defense are likely to vary jointly with the characteristics of the resource. Moreover, because the behavior during encounters depends on both individuals' cost-benefit ratios, a general theory will need to consider the relative advantages of different agonistic tactics by both opponents. The key is probably in identifying those circumstances in which the benefits of a resource for a resident



outweigh its attraction to intruders. Along these lines, in "Spacing in Relation to Resources" below, we consider conditions that make the benefits of a resource greater for a resident than for intruders.

#### ANALYSIS OF CONTINGENCIES IN SOCIAL INTERACTIONS

An approach that explicitly analyzes agonistic behavior as an interaction, in which the effect of an individual's behavior is contingent on its opponent's behavior, employs game theory and the concept of an evolutionarily stable strategy (ESS) (Maynard Smith and Price, 1973). An ESS is one invulnerable to invasion by any mutant strategy; the expected benefit from a strategy when matched against itself must exceed the benefit when matched against any other strategy.

Particularly relevant to spacing behavior are contests with "uncorrelated asymmetry" (Maynard Smith and Parker, 1976; Maynard Smith, 1974b, 1976), in which the opponents differ in some way not associated with the "payoff" (the benefits that accrue to the winner of an interaction) or the "resource-holding potential" (an individual's inherent ability to win if it tries, as opposed to its strategy of how much and when to try). In particular, Maynard Smith analyzed a situation in which the asymmetry of opponents might involve ownership of a resource. In this situation, an ESS could result from conventional settlement of contests by escalating a contest ("hawk" strategy) when an owner and retreating immediately ("dove" strategy) when not, provided that all individuals are equally likely to play either role and provided that the escalating strategy is continued to a sufficient degree of risk (the expected gain in encounters between escalators must be negative). Thus, territorial defense by conventional behavior could evolve in spite of a lack of correlation between prior residence and either the benefits of ownership or inherent abilities to win encounters.

Advantages of prior ownership could also explain the evolution of conventional behavior in territorial interactions (Maynard Smith, 1976). Consequently, the occurrence of conventional interactions does not necessarily establish that they are "uncorrelated asymmetric" interactions. In fact, territorial and nonterritorial individuals in a population, or early and late arrivers, or residents in optimal and in suboptimal areas, often differ in age, so that one might expect correlations between prior residence and inherent abilities to win encounters. In stable populations of relatively long-lived animals, older individuals tend to invest more energy in reproduction than younger ones, and their additional experience might also favor them. Furthermore, residents might reap greater benefits from an area, at least for the immediate future, than newcomers, provided that an individual's experience in an area increases its benefit. The stipulation that individuals are equally likely to play either role in asymmetrical contests also seems unlikely to apply; age in particular often correlates with prior residence in territorial contests. In fact, the example cited by Maynard Smith and Parker (1976) to illustrate conventional behavior in territorial interactions, Krebs's (1971) study of great tits (*Parus major*), illustrates well the correlation of age with residence in an optimal, as

opposed to a less advantageous, location. The failure of young birds in poorer habitats to challenge older birds in better habitats might well result from the correlations of this asymmetry.

Relationships between territorial neighbors might meet the requirements for an uncorrelated, asymmetrical contest better, although Maynard Smith and Parker (1976) dismiss the possibility. Here, individuals might take the roles of intruder and resident equally frequently, and this asymmetry might in fact lack association with payoffs or resource-holding potentials. Purely conventional behavior seems to be the rule in encounters between an intruding neighbor and a resident. At the boundary, or when a boundary has not yet been established by new neighbors, the contest is no longer asymmetrical, and in these circumstances, encounters between neighbors seem closer to Maynard Smith's "war of attrition."

Game theory is notably successful in predicting the global properties of animal conflicts and holds considerable promise for formulating more precise predictions about differences in spacing behavior between species and populations. It remains unclear, however, just what form of "game" animals are really playing in spacing interactions. Certainly, they are not playing repeatedly against the same opponent with the same payoffs and resource-holding potentials. Instead, they are playing a series of individuals with differing resource-holding potentials and differing payoffs, and even their own resource-holding potential varies with age or experience in past interactions.

Perhaps of special importance is the problem of treating games in which information is imperfect (Maynard Smith and Parker, 1976). Real animals almost never know their opponent's payoffs or resource-holding potentials precisely and have to estimate them from indirect information transmitted by the opponent. It seems likely that many spacing behaviors—and spacing signals, in particular—serve to obtain the information necessary to refine estimates of payoff and opponent's resource-holding potentials or to confound an opponent's attempt to do the same. Strategies for obtaining this information are surely an integral part of the "game." Intuitively, it seems clear that evolutionarily stable strategies depend on the accuracy of such estimates, yet only a beginning has been made on this difficult problem (Maynard Smith and Parker, 1976). What factors determine, in any real case, where the balance lies between bluffing and calling bluffs or between mutual avoidance and overt aggression? What factors determine the optimal area or effectiveness of defense? Game theory remains to be applied to these questions.

#### SPACING IN RELATION TO A RESOURCE: INDIVIDUALS WITH BASES OF OPERATION

In another approach to the evolution of spacing patterns, the spatial relationships optimal for resident individuals in a population at saturation density are derived from the spatial distribution of food in the environment. Two related calculations along these lines have shown that dispersed, stable resources, exploited by animals foraging radially from a base of operations, such as a nest or cache, favor dispersed ranges without overlap, rather than aggregations. Horn (1968) imagined an environment in which food occurred predictably in equal amounts at regular intervals. He could easily show that the distance a bird traveled

to bring a given amount of food to its nest was less when individuals had ranges without overlap than when several individuals foraged from the same base. A similar demonstration by Smith (1968) showed that squirrels collecting seeds for caching at a central location traveled shorter distances if each occupied exclusive ranges than if two shared the same range. In essence, when individuals aggregate under these conditions, an individual must travel farther to collect the food to replace that already removed by others from locations close by.

The inverse theorem, however, seems not to follow, in spite of Horn's (1968) deductions. Clumped resources that vary in space and time are not necessarily more efficiently exploited by aggregated individuals foraging from a base than by dispersed ones, at least from the sole standpoint of the expected distance traveled per unit of resource. Horn's deductions for a habitat with a variable distribution of food pertain only to habitats with dimensions similar to the maximum ranges of foraging individuals. Horn imagined a habitat of 16 locations for food, at each of which enough food for 16 individuals appears with a probability of  $\frac{1}{16}$  in each unit of time. In these circumstances, individuals travel the least distance per unit of food on the average if they all are based in the center of the habitat (Horn, 1968). A base near one edge requires that an individual spend some of its time foraging near the opposite edge; with a base near the center, an individual never has to travel that far for food. In essence, a resource with high spatiotemporal variation is not efficiently exploited from a base near one edge of a block of habitat.

Consider a similar habitat, in which enough food for 16 individuals appears at each location with a probability of  $\frac{1}{16}$  per unit of time, but extending indefinitely, unlike Horn's example. When the dimensions of the habitat greatly exceed the foraging ranges ( $F$ ) of individuals, all locations greater than a distance  $F$  from an edge have equal accessibility to the patches of food. In this case, widely overlapping but dispersed activity fields have the same efficiency as aggregations.

Brewer's blackbirds (*Euphagus cyanocephalus*) in central Washington nest beside lakes, around which they feed on concentrations of emerging odonates (Horn, 1968). The aggregation of their nests, insofar as access to food is the determining selection pressure, is as much a consequence of the large-scale restriction of a predictable food source to the shores of one moderate-sized lake as of the small-scale unpredictability in the location around the lake shore at which food accumulates on any one day. Aggregation, as Horn (1968) suggested, might also confer evolutionary advantages in protection from predators and in communication about the locations of patches of food.

These calculations suggest three principles about the dispersion of individuals in relation to the dispersion of a resource, when individuals forage from a base of operations and no selection pressures affect the dispersion of individuals other than the effort necessary to transport the resource to the base:

1. If the availability of the resource does not vary appreciably in space and time, evenly dispersed activity fields without overlap provide the most efficient spacing.
2. If the availability of the resource varies appreciably in space and time and if the habitat has dimensions approximating the foraging ranges of individuals, then

aggregated bases of operation near the center of the habitat provide the most efficient spacing.

3. If the availability of the resource varies as above and the habitat has dimensions greatly exceeding the foraging ranges of individuals, then *either* aggregated bases of operation *or* evenly dispersed but widely overlapping activity fields provide equally efficient spacing.

The distinction between the conditions for Principles 2 and 3, which hinges on the relationships between the dimensions of a patch of habitat and the foraging ranges of individuals, depends on the distribution of the shortest distance between sites at which the resource is simultaneously available. This distribution determines how large the diameter of an individual's activity field must be to encompass a productive site with a sufficiently high probability in any unit of time.

The distinction between stable and variable resources, which differentiates Principle 1 from the other two, hinges on the relationship between an individual's needs ( $N$ ) in some appropriate time period ( $\Delta t$ ) and both the amount of resource available at a particular site ( $R$ ) and the variation in  $R$  from one interval  $\Delta t$  to the next. The central question is whether or not an individual, in an environment at saturation density, can get by on a fixed set of sites equal to its own share of the environment. If so, evenly dispersed bases are most efficient. An individual can manage in this way only if its own share of sites has a sufficiently high probability of having enough resource to meet its needs continually. For some simple conditions, the sufficiency of each individual's share of sites increases as the availability of the resource becomes more evenly distributed across sites and time periods (appendix).

This discussion is well illustrated in qualitative terms by a comparison of two species of birds that consume insects of the litter on forest floors: ovenbirds (*Seiurus aurocapillus*) (Stenger, 1958; Stenger and Falls, 1959; Zach and Falls, in press) and bicolor antbirds (*Gymnopithys bicolor*) (Willis, 1967). Ovenbirds, which remain primarily within their own territories, search for insects scattered in the forest litter. The food available ( $R$ ) at any one site is certainly less than an individual's needs during a foraging bout, but at any one time, numerous locations within a territory have food. Sizes of territories vary from habitat to habitat in accordance with the abundance of insects in the litter.

Bicolor antbirds catch insects flushed from the litter by advancing columns of army ants in neotropical forests. Because they rely entirely on this food supply, their food is available only in small patches widely scattered in the forest in locations that are relatively unpredictable from week to week. At an army ant raid, though, there is enough food for many individuals ( $R > N$ ), and, in fact, several pairs of this species and individuals of many other species often gather. Pairs of bicolor antbirds occupy regularly spaced activity fields with extensive overlap. The dimensions of the habitat are clearly greater than the sufficient diameter of an activity field, so Principle 3 applies. Evidently, some other selection pressure, perhaps an advantage of dispersed, cryptic nests in avoiding predation, favors dispersed spacing rather than aggregations. Note that the demand for resources within relatively large areas is set by the distances between the centers of individuals' activity fields as well as by the degree of overlap (Willis, 1967).

In summary, an extensive habitat with unpredictable patches of food places no constraints on the dispersion of individuals' bases of operations: overdispersed and aggregated bases are equally efficient in minimizing travel time. Other factors affect the spacing of bases in such an environment. A habitat with sparse, evenly distributed food, on the other hand, specifically favors overdispersed bases of operation, because regular spacing minimizes travel time from the base to locations with food. For such populations to evolve aggregated bases, selection for aggregation for other reasons must more than compensate for the disadvantage of increased travel time.

#### SPACING IN RELATION TO RESOURCES: A GENERAL PERSPECTIVE

The preceding principles depend strongly on the assumption that each individual has a fixed base of operation from which it forages, such as a nest, a den, or a cache. These principles relate the optimal dispersion of individuals' bases of operation to the dispersion of a limiting resource. In this situation, animals adjust one constraint on their activity fields, the locations of their bases, to another constraint, the dispersion of a limiting resource. In fact, this situation is a special case of the problem of multiple constraints on individuals' spacing.

S. Altmann (1974) has analyzed multiple constraints on activity and isolation fields, including the effects of two or more limiting resources with different dispersions, such as sleeping sites, food, and water, in a comparison of baboons (*Papio*) in Amboseli and Nairobi National Parks, Kenya. He suggested, among other principles, that overlap of home ranges is determined by the spacing of those essential resources most restricted in their distribution. For instance, baboon troops overlap at large but scarce waterholes or sleeping groves. In Amboseli, where sleeping groves and water holes are less evenly distributed than at Nairobi, baboon troops occupy activity fields with more overlap than do troops in Nairobi. This principle, however, specifies only a *minimum* extent of home range overlap.

Consider what might influence the spacing of individuals in relation to a resource, without other constraints on movements. If regular dispersion is favored, what influences the degree of isolation within individuals' activity fields? In particular, what favors exclusive activity fields as opposed to overlapping ones?

Individuals with no other constraints on their movements would minimize their travel times if they could match their activity fields to the dispersion of food in their environment. When  $R$  (the amount of resource available at a site) is not much greater than  $N$  (an individual's needs), individuals should forage independently from one food item or patch to the next. However, when clumps of food contain amounts substantially greater than  $N$ , individuals should aggregate; the number of individuals per clump of food should vary from population to population or from time to time with the expected amount of food per clump. Spider monkeys (*Ateles belzebuth*) show such adaptability in spacing (Klein and Klein, 1975).

Thus, when the availability of a limiting resource varies appreciably across locations and time, individuals should occupy widely overlapping activity fields. This prediction resembles Principle 3 above: either with or without bases of

operation, individuals exploiting a variable resource should occupy widely overlapping activity fields (see also Waser, 1976, and appendix). The analog of Principle 1, when individuals lack bases of operation, is less clear.

What might favor exclusive activity fields for individuals foraging solitarily in an environment with an evenly dispersed, stable resource? Consider an animal that has traveled a certain distance in one direction and now faces a decision of whether to proceed or turn back. The optimal decision depends in part on what it "knows" about the current state of the area it just passed through in comparison to the area ahead. If it knows that the availability of the resource is low in the area behind, then proceeding would be preferable.

There are several ways that a foraging animal could know that the availability of a resource is low in an area just searched: the animal might already have removed most of the resource and know that renewal rates are low; it might have encountered little and know that rates of encounter are correlated at nearby locations or in successive time intervals at any one location; or it might know that the behavior of prey individuals changes to reduce their vulnerability for a while after detecting a predator. Of course, these sorts of "knowledge" could result either from the animal's own experience or from inheritance of adapted behavioral tactics. The first and third of the preceding possibilities have been termed exploitation depression and behavioral depression of a resource as a consequence of an animal's foraging activities (Charnov, Orians, and Hyatt, 1976).

Any persistent depression or scarcity of the resource in the area immediately to the rear favors continuing forward. The animal's optimal procedure thus depends on whether some advantage of turning around can compensate. On the other hand, if the availability of food fluctuates rapidly at any one site or renews rapidly after exploitation, rates of encounter with food might have little serial correlation over relatively brief periods. In this case, moving ahead or to the rear could prove equally fruitful.

Consider first the case in which turning around has no sufficient advantage. If it is disadvantageous for an individual to backtrack, it will probably also prove disadvantageous for two individuals to search near each other. The optimal spacing would consist of widely overlapping activity fields, regular olfactory marking or acoustic advertisement while moving, and immediate avoidance of other individuals' paths or locations, behavior like that of cheetahs (see the second section). If the cumulative searching by all individuals at a locality were disproportionately low in relation to the availability of the resource there, it would prove advantageous for one or more individuals to shift their activity fields to include more time there. In such cases, regular dispersion of the widely overlapping activity fields would equalize the demands on resources at different sites over large areas.

In contrast, consider the consequences when turning back has advantages. Suppose, for instance, that an individual can find food more rapidly in familiar areas than in strange ones. Then knowledge of good places to find food farther to the rear could compensate for the disadvantages of backtracking through recently searched areas immediately to the rear. Furthermore, if familiarity with an area enhances ability to find food reliably, an individual might face the disadvantage of competing with a more efficient individual in the area ahead. So when familiarity

with an area increases an individual's efficiency in exploiting the limiting resource there, an individual would do best to stick near familiar areas and avoid areas more familiar to another individual.

Few studies have explicitly investigated the effects of an animal's familiarity with an area on its ability to find food there, although such an effect is likely to influence foraging efficiencies for many species that search for cryptic or sparsely distributed food. "Search images" or spatial restrictions on searching (see Krebs, 1973, and this volume) would permit individuals to concentrate on the kinds of food or locations that maximize foraging success in local areas. Individuals familiar with an area could monitor small patches of renewing resources (Zach and Falls, 1976c). Individual differences in prey selection, as Southern (1954) reported for neighboring tawny owls (*Strix aluco*) in the same wood, suggest these consequences of familiarity with an area. One direct confirmation that familiarity increases foraging success in an area comes from a study of pinioned ovenbirds confined to fenced enclosures on the forest floor (Zach and Falls, 1976a,b). On introduction to an enclosure, individuals with earlier experience there returned immediately to the previous locations of patches of food.

When familiarity with an area increases foraging success, it would prove advantageous for neighboring individuals to establish clear boundaries and avoid each other's areas. Of course, these areas must reliably include enough of the limiting resource to sustain an individual or group of individuals (see appendix). Consequently, optimal spacing in this case would consist of activity fields with little overlap and isolation fields with pronounced convexity. The less the advantage of familiarity in exploiting the resource, the more often excursions across the boundary might occur, and avoidance would have less importance in the isolation of individuals from their neighbors.

Renewal rates of a limiting resource also influence the relative advantages of proceeding ahead or turning back. As noted above, the costs of backtracking are low when renewal rates are high. Consequently, a slight advantage of familiarity with an area would favor exclusive activity fields when renewal rates are high, while much greater advantages would be necessary when they are low.

These considerations lead to the major conclusion that a stable, evenly dispersed resource does not necessarily favor exclusive activity fields for animals without bases of operation. This conclusion stands in contrast to our earlier one for animals with bases. In the absence of bases of operation, exclusive activity fields evolve only when each individual realizes an advantage from confining itself to a set of sites equal to its share at saturation density. This stipulation normally requires an advantage to turning around while foraging. In a sense, a base of operations—a nest, den, or cache—creates the clearest sort of advantage for turning back. Our reasoning above suggests that any advantage of site attachment, such as an advantage of familiarity with an area in exploiting a limiting resource, could favor returning after an individual had proceeded some distance in one direction.

For animals whose spacing is constrained by a single limiting resource, the following two principles apply, in place of those stated above:

4. If the availability of the resource varies appreciably in space and time, then

widely overlapping activity fields provide the most efficient spacing; individuals or cohesive groups might aggregate temporarily, depending on the amount of resource in a particular clump.

5. If the availability of the resource does not vary appreciably in space and time, then *either* overlapping *or* exclusive activity fields provide the most efficient spacing, depending on whether or not a sufficient turning-around advantage exists; individuals or cohesive groups should forage solitarily.

This approach to understanding the evolution of spacing has focused on the relations of neighboring, resident individuals. Our reasoning has suggested that either overlap or exclusiveness of neighbors' activity fields could prove mutually advantageous for neighbors, depending on spatiotemporal variability in the resource and any turning-around advantage. The argument has proceeded in two steps. The first question is whether or not an individual, in a population at saturation density, can get by on its share of sites or area. If it can, a second question is whether or not there are reasons for an individual to confine itself to this minimal set of sites. These arguments suggest that established neighbors should engage only in ritualized encounters, with outcomes predictable in advance, either mutual avoidance or ritualized encounters at established boundaries. Once residents have occupied the environment at saturation density, strangers should evoke greater hostility than established neighbors, a phenomenon verified by field experiments (see the second section).

#### SPACING IN RELATION TO RESOURCES: EXAMPLES

The preceding conclusions apply well to the arboreal primates of the Kibale Forest in Uganda (Struhsaker, 1975, 1978; Struhsaker and Oates, 1975; Oates, 1976; Rudran, 1976; Waser, 1976), five species that differ widely in the characteristics of their movements, their group size, the overlap of activity fields, and intergroup encounters (Table III; Struhsaker, 1975).

Of these five species, the mangabey uses the most clearly patchy resource; it feeds primarily at fruiting fig trees (*Ficus*), which at any one time are widely and irregularly scattered in the forest. Information on the density and fruiting of fig trees in the Kibale Forest suggests that the activity field of a mangabey group includes enough trees to ensure, with negligible risk, a continuous supply of food. As expected for a resource with high temporal and spatial variability (see appendix and Waser, 1976), activity fields that are large enough to ensure a continuous supply for one individual or a cohesive group will often include enough for others as well.

The two species of colobus in the same area contrast in their spacing (Struhsaker and Oates, 1975; Struhsaker, 1975). The red colobus (*Colobus badius*) takes a diet of growing leaves and shoots plus some fruit and flowers. These items tend to be available in abundance on a given tree or species of tree for a short period during the year, so that red colobus groups must exploit a variety of food sources. In addition, this species seems to prefer a varied diet even when one kind of food is locally abundant (Clutton-Brock, 1975). Although the temporal and spatial variation in the food sources of red colobus are not so clear as in the figs that



mangabeys depend on, some of the important food trees are clumped within the habitat, and their phenologies suggest substantial temporal variation in availability (Struhsaker, 1975). Red colobus seem to provide a second example of a species with variable resources and widely overlapping activity fields. Moreover, to the extent that this species concentrates on short-lived resources with low renewal rates, there is little premium on turning back.

Black-and-white colobus, in contrast, consume a less diverse diet, mostly leaves of a few species of common trees, which are continuously available in relatively small areas throughout the year (Oates, 1976). In addition, they can subsist during lean periods primarily on mature leaves. Although neighboring groups have appreciable overlap in their activity fields, the overlap is much less than for red colobus or mangabeys. A group probably depletes the available food in one place only slightly before moving on, so there is probably little disadvantage to turning back. Consequently, for black-and-white colobus, only a slight turning-around advantage, perhaps from familiarity with the best shelter, paths, or food trees, would compensate for the slight disadvantage of crossing recently exploited areas.

The two species of *Cercopithecus* in the Kibale Forest have largely exclusive activity fields and include insects as an important component of their diets (Rudran, 1976; Struhsaker, 1975, 1978). Groups of blue monkeys (*C. mitis*) move more or less straight ahead during any one day, over a route that amounts to

TABLE III. SUMMARY OF MOVEMENTS, SPACING, GROUP SIZE, AND INTERACTIONS BETWEEN GROUPS FOR FIVE ARBOREAL PRIMATES IN THE KIBALE FOREST, UGANDA<sup>a</sup>

Species	Usual group size	Approximate mean area of activity field (ha)	Extent of overlap by neighboring groups	Nature of encounters between groups
Gray-cheeked mangabey ( <i>Cercocebus albigena</i> )	6-28 <sup>b</sup>	400	Wide	Short-term avoidance independent of location
Red colobus ( <i>Colobus badius</i> )	12-80 <sup>b</sup>	35-50	Wide	Intergroup supplantations independent of location
Black-and-white colobus ( <i>C. guereza</i> )	3-15	15	Intermediate	Long-range acoustic communication; infrequent short-range interaction
Blue monkey ( <i>Cercopithecus mitis</i> )	10-28	100	Little	Long-range acoustic communication; infrequent short-range interaction
Red-tailed monkey ( <i>C. ascanius</i> )	15-35	25	Very little	Regular short-range interactions

<sup>a</sup>After Struhsaker, 1975.

<sup>b</sup>Usually two or more adult males per group.

appreciably less than the diameter of a typical activity field. Red-tail monkeys (*C. ascanius*) move back and forth in any one day, over a route that is generally much longer than the diameter of a typical activity field. Both species take a highly diverse diet, but the inclusion of insects might mean that groups familiar with their foraging areas would have a distinct advantage. These two species thus exemplify the case of exclusive activity fields in association with evenly dispersed resources and an advantage of familiarity with foraging areas.

The diets and foraging techniques of blue and red-tailed monkeys suggest a plausible explanation for the differences in their daily movements. Blue monkeys take large, apparently sedentary insects from foliage without special movements, while red-tails take many smaller, active insects, which they often catch with a sudden grab. The lower abundance of large items suitable for blue monkeys and the lower renewal rates of these items could favor lower rates of return to particular areas within the monkeys' activity fields. For red-tails, the renewal of suitable items in accessible locations probably proceeds much more rapidly, so that more frequent returns to a particular area become possible.

The differences in daily movements of these two species might, in turn, explain the differences in the nature of agonistic interactions between neighboring groups. Blue monkeys only infrequently engage in short-range encounters with their neighbors, while red-tails regularly encounter their neighbors at short range (Rudran, 1976; Struhsaker and Leland, 1979). A species with short daily movements in relation to the diameter of its activity field would incur a substantial cost in traveling to and from boundaries especially to encounter neighbors at short range, a circumstance that might favor long-range acoustic interactions for maintaining exclusive activity fields. In addition, acoustic advertisement at long range for a restricted period each day can provide reliable information on the positions of groups with respect to their boundaries throughout the day. In contrast, when a group's movements take it near boundaries repeatedly during the day, short-range interactions with visual contact become necessary to define boundaries, yet they incur little extra cost in travel.

With the possible exception of red colobus, none of the primates of Kibale seems to exemplify the evolution of overlapping activity fields for a dispersed resource without a sufficient turning-around advantage. Possibly, long residence in an area normally results in sufficient advantages from familiarity with foraging sites, shelter, or routes of travel, so that exclusive activity fields would prove optimal for dispersed resources.

The situation might be different for transient individuals. The shorebirds studied by Goss-Custard (1970) in migration and winter exemplify widely overlapping movements in exploiting a dispersed resource, invertebrates of intertidal mudflats. This resource might also change in its microdistribution from one tide to the next, a circumstance that would further reduce the possibility of a bird's familiarizing itself with foraging areas. Although migrant sandpipers sometimes defend small areas or localized food sources (Hamilton, 1959), most species on migration or in winter, including those studied by Goss-Custard, do not. As Goss-Custard demonstrated, organisms living near the surface withdraw into the mud and become unavailable to surface-feeding sandpipers for a period of three to five

minutes after a bird walks past. Goss-Custard did not determine the extent of this effect on either side of a walking sandpiper beyond a minimum distance of 4 cm. This temporary reduction in the availability of prey behind a foraging sandpiper favors dispersion of individuals, in order to minimize mutual interference, and also discourages turning around by a foraging individual. In fact, species that feed on organisms near the surface tend to scatter more widely while foraging. Those that probe deep into the mud standardly form tight flocks while foraging.

Species feeding on organisms near the surface do not consistently turn less frequently than those feeding on deeper organisms; however, the former species move much faster. Consequently, although Goss-Custard did not analyze his data in this way, species feeding on organisms near the surface apparently make fewer turns per meter as they forage.

Thus, wintering sandpipers that exploit a dispersed, gradually renewing resource avoid each other, seldom backtrack while foraging, and use widely overlapping areas. They exemplify overlapping activity fields for utilizing a dispersed resource in the absence of a sufficient turning-around advantage. Those sandpipers that exploit a less predictable resource avoid each other less and turn more per distance traveled.

#### OTHER INFLUENCES ON THE EVOLUTION OF SPACING BEHAVIOR

The spatial and temporal distribution of a limiting resource in an environment, as we have seen, determines the disadvantages of foraging near other individuals or in areas used by others. The possibilities of such interference, however, are not the only consideration in predicting the optimal spacing of individuals. In addition, opportunities for cooperation in obtaining food and avoiding predation might vary with individuals' spatial relationships. The optimal spacing for individuals in a particular population might thus require a compromise between possibilities for reducing interference and increasing cooperation among individuals.

If nearby individuals can cooperate in locating resources or capturing prey, aggregation rather than dispersion would have advantages (see Krebs, this volume). Aggregations also sometimes have advantages in detecting cryptic predators or surprise attacks and in reducing the risk of mortality once a predator is detected by means of coordinated activities of the group, such as mobbing the predator to repel it (Kruuk, 1964; Hamilton, 1971a; Vine, 1971; Pulliam, 1973; Siegfried and Underhill, 1975).

On the other hand, aggregations often attract a predator's attention more than solitary individuals and carry the risk of disproportionate loss when predators can easily attack several individuals at once or in close succession. Tinbergen and his collaborators (Patterson, 1965; Tinbergen, Impekoven, and Franck, 1964; Tinbergen, 1967) have clearly shown the counteracting effects of aggregation and dispersion of nests in reducing predation within colonies of birds.

Recent evidence suggests that kinship, a factor rarely considered in the control of spacing patterns, can affect spacing behavior in some striking ways. As would be expected from theoretical arguments (Hamilton, 1971b), sea anemones

display aggression between clones but not within them (Francis, 1973). At the opposite end of the phylogenetic array, among siamang (*Symphalangus syndactylus*), the territory of a male offspring is often carved out of the parents' range without obvious interference from them (Aldrich-Blake and Chivers, 1973). The inheritance of part of the natal home range by offspring has been suggested as a major evolutionary route to sociality (Brown, 1964; Eisenberg, 1977; Woolfenden and Fitzpatrick, 1978). The phenomenon is increasingly reported in organisms traditionally regarded as solitary, including white-crowned sparrows (Baker and Mewaldt, 1978), sloths (Montgomery, in press), bears (Herrero, 1978), and leopards (Bertram, 1974). The persistence of kin as neighbors in solitary species will require explicit consideration in future evolutionary discussions of spacing phenomena.

### CONCLUSION

A general theory of adaptations in spacing behavior must predict not only the distribution of activity fields in space but also the optimal form of an individual's activity, aggression, and isolation fields. For some species or populations, one or a few ecological parameters accurately predict the optimal parameters of spacing behavior. For other species, the ecological parameters undoubtedly have complex correlations among themselves and interacting effects on spacing behavior. Adaptations in spacing behavior depend on at least the following ecological variables: the dispersion in space and time of one or more limiting resources; the effects of familiarity with an area on an individual's ability to exploit a limiting resource; the existence or not of a base of operations, such as a nest, a den, or a cache; the effects of proximity to other individuals on an individual's ability to exploit a limiting resource; and the effects of proximity to other individuals on the risks of predation.

### APPENDIX

In considering the optimal spacing of animals, either with or without bases of operation, we encountered the question of whether or not an individual's share of sites at saturation density is enough to provide a reliable supply of a limited resource. If a set of locations equal to an individual's share at saturation density can provide, with a sufficiently high probability, the individual's needs in any one time period, then any form of site attachment, either a base of operation or some other sufficient turning-around advantage, would favor individuals that restricted their foraging to that minimal set of locations.

Our task, then, is to analyze the relationship between the temporal and spatial variability of a resource and the probability that an individual's share of sites will include enough resource in any one time period. First, following Horn (1968), choose a spacing of sites (or dimensions of quadrats) and duration of time intervals  $\Delta t$ , so that the availability of the resource varies independently across sites and

time intervals. Then let  $D$  = the density of sites,  $\bar{R}$  = the mean availability of the resource across sites at any one time and across time at any one site, and  $N$  = an individual's needs (in the same units as  $R$ ) in one time period. Then, the saturation density of individuals will be  $\bar{R}D/N$ , and an individual's share of sites at saturation density will equal  $N/\bar{R}$ . Over the long term, regardless of whether resources are stable or variable,  $N/\bar{R}$  sites will average an amount  $N$  of resource, enough for one individual in one time period.

The average availability of the resource is not our principle concern; instead, we want to know the probability that  $N/\bar{R}$  sites will have enough resource for an individual *in any one time period*. Assume for simplicity, as Horn (1968) did, that each site has either an amount of resource  $R$  or nothing at any time period  $\Delta t$ . Then, each site has a probability of  $\bar{R}/R$  that resource is available in any  $\Delta t$ . The probability that a set of  $N/\bar{R}$  sites will include  $A$  sites with resources available in any  $\Delta t$  is specified by the binomial distribution for  $A$  successes in  $N/\bar{R}$  trials when the probability of success per trial is  $\bar{R}/R$ .

The number of sites that will satisfy an individual's needs in any  $\Delta t$  depends on whether  $R$  is greater or less than  $N$ . When  $R > N$ , an individual needs to visit, in any  $\Delta t$ , only one site with the resource available. The question then is whether or not  $N/\bar{R}$  sites, an individual's share at saturation density, will include *at least one* with the resource during any  $\Delta t$ . This probability, available from the cumulative binomial distribution, approaches 1.0 as  $\bar{R}/R$  approaches 1.0. In contrast, when  $\bar{R}/R$  is small, an individual's share of sites at saturation density would have a low probability of including enough resource during any one time period. Yet, if  $R$  is greater than  $N$ , when the resource is present at a site, there is more than enough for one individual. In addition, the probability that two or more sites will have the resource, among a set of  $N/\bar{R}$  sites, would be appreciable. Under these conditions, overlapping ranges would prove most efficient, whether or not individuals had bases of operation.

When  $R < N$ , then no one site can provide enough resource for an individual in any  $\Delta t$ . Each individual needs to collect the resource at  $N/R$  sites in each  $\Delta t$ . For

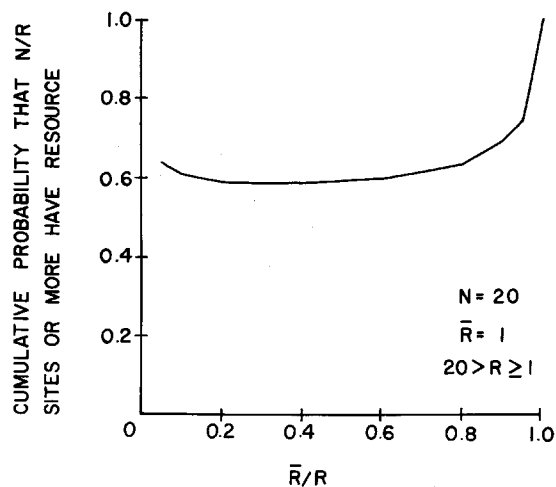


Fig. 6. Effects of spatiotemporal variation in the availability of a limiting resource on the probability that an individual's share of sites will include at least enough resource in a time period,  $\Delta t$ .  $N/\bar{R}$ , an individual's share of sites at saturation density;  $\bar{R}/R$ , the probability that an amount  $R$  of resource is available at a site in  $\Delta t$ ;  $N$ , an individual's needs in  $\Delta t$ ;  $R < N$ . For this example,  $N$  is held constant, while  $R$  varies. See text for further explanation.

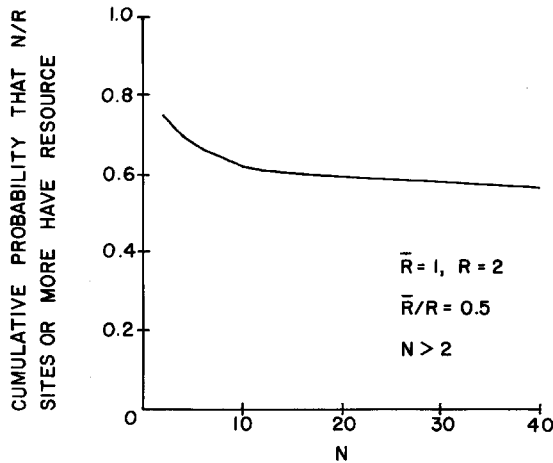


Fig. 7. Effects of  $N$ , an individual's or a cohesive group's needs in any time period, on the probability that the individual's or group's share of sites will include at least enough resource in a time period.  $N/R$  and  $\bar{R}/R$ , as in Figure 6;  $R < N$ . Here  $R$  is held constant, while  $N$  varies. See text for further explanation.

any given  $\bar{R}$  and  $N$ , which specify an individual's share of sites  $N/\bar{R}$ , a decrease in  $R$  will increase both the probability of a resource at any one site,  $\bar{R}/R$ , and the number of sites with resource needed to support an individual in any  $\Delta t$ ,  $N/R$ . These changes have counteracting effects on the cumulative probability of at least  $N/R$  successes in  $N/\bar{R}$  trials when each trial has a probability of success  $\bar{R}/R$ . Examples taken from tables of the cumulative binomial distribution indicate that the probability of having enough resource within an individual's share of sites varies remarkably little over wide ranges of  $\bar{R}/R$ , for a given  $N$  and  $\bar{R}$ , or over wide variation in  $N$ , for a given  $\bar{R}/R$ . The probabilities vary between 0.5 and 0.75, until  $\bar{R}/R$  approaches very close to 1.0 (Figures 6 and 7). Consequently, when an individual must collect the resource from a number of locations to fill its needs, wide variation in the predictability of resource at each site has little effect on the probability that an individual's share of sites will include enough in any one time period. Overlapping activity fields would prove necessary unless the presence of the resource were *highly* predictable.

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