

Social Organization and Foraging in Emballonurid Bats

III. Mating Systems

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Summary. 1. A general model of mating system evolution in mammals is developed, which takes into account the different male strategies of resource defense, female group defense, and male mating aggregations. The critical environmental variables determining differential defensibility of females and resources are identified by generalizing the resource defense model of Orians (1969). The model is then applied to available data on African antelopes (Jarman, 1974) to establish a set of hypothetical relations between certain patterns of habitat use and mating structures. The resulting relations are only likely to apply to species in which food determines female dispersion and in which any resource defense exhibited by males is directed towards food supplies.

2. The relations developed for antelopes are then compared to recently published data on mating systems in five neotropical emballonurid bats (Bradbury and Vehrencamp, 1976a).

3. Antelopes and the bats are found to share the following features. Species living in wet and stable forests tend to be fine-grained socially and to have groups consisting of monogamous pairs or nested male-female territories. Species in more seasonal habitats show an inverse relation between the size stability of groups and the duration of use of a given foraging site. As the model predicts, in both groups resource defense occurs where groups are least stable and female defense where groups are most stable. Also as the model predicts, the numbers of females accessible to each male and the number of reproductive males per group can be anticipated in each of the two taxa wherever sufficient data for the critical variables are available.

4. Antelopes and bats differ in the following ways. Whereas body size is a good predictor of antelope habitat use and social dispersions, it is a poor predictor for emballonurid patterns. Similarly, although the numbers of females per male generally increase with group size in antelopes, this correlation does not hold for the bats in this study. These differences lead to the conclusion that application of the general model cannot be simplified

by measurement of a few variables such as body size or group size, but instead will generally require actual measurements of the critical resource dispersion parameters in the field.

Introduction

The form of most animal social systems can be characterized by specifying the social dispersion (i.e., group size and spacing), the mating system, and the patterns of juvenile dispersal and/or retention. Several authors have recently suggested that selection operates initially on social dispersion and that subsequent evolution of mating systems can only occur within the options allowed by that social dispersion (Jarman, 1974; Alexander, 1974). A similar notion implicitly underlies those models of mating system evolution which rely on resource distributions as environmental determinants (e.g., Orians, 1969). In a prior paper, we analyzed field data on several species of neotropical emballonurid bats and argued that social dispersion in these species was primarily determined by a passive mapping of the animals onto their food dispersion (Bradbury and Vehrencamp, 1976b). In this paper, we wish to utilize the same data, (Bradbury and Vehrencamp, 1976a), to see (1) to what degree prior determination of social dispersion limits mating options in these species, and (2) whether current models of mating system evolution are sufficient to explain the observed diversity of emballonurid mating structures. Methods of data collection can be found in Bradbury and Vehrencamp (1976a).

Form and Process in Mating System Evolution

It will be important to our analysis of emballonurid mating patterns to outline briefly the types of mating systems one might expect to find in mammals, and the ways in which environmental contexts have been invoked as determinants of one type or the other. A "classical" taxonomy of mammalian mating systems would distinguish between monogamous pairs, harems, groups of females tended by several adult males (hereafter called "multi-male groups"), and leks. We feel that a more useful system can be based upon the strategies available to males. We distinguish three broad categories:

1. Resource Defense. Males establish territories containing some resource (food, water, nesting or roosting sites, etc.), required by females. Exclusion of other males and admission of females only on condition of biased mating access are two ways that such territorial males might gain in fitness. Examples include many of the savannah antelopes of Africa (Jarman, 1974).

2. Female Defense. If it is advantageous to form stable groups as an anti-predator device, to increase foraging efficiency, or to share in parental duties, males may be able to exclude or dominate other males and thereby enhance their own mating success. Mammalian examples include some baboons and ungulates such as the eland and African buffalo (Kummer, 1968; Jarman, 1974).

3. *Male Mating Aggregations.* Males may aggregate at traditional or species-specific sites and be visited by females only for mating. If females are able to approach the aggregation and make a choice of mate, we may call the aggregation a "lek". An example would be the Uganda kob (Buechner and Schloeth, 1965). If an approaching female is mobbed by males and no mating choice is possible, we may call the aggregation a "mating swarm" after the corresponding behavior in flying insects (Downes, 1969). The latter behavior appears to occur in some temperate bats prior to hibernation (Fenton, 1969).

The important difference between this system and a more classical listing is that it redirects the focus away from the *form* of the mating system towards the conditions which have given rise to these forms. This shift is intentional because it helps to clarify the fact that the same mating structure may arise by several different routes. For example, harems may arise either by male defense of a resource to which groups of females come (e.g., antelopes), or by the appending of an adult male to an existing female group and defense of the group from other males (e.g., Burchell's zebras). It is also the case that within any one strategy, say defense of female groups, different mating forms may arise, e.g., harems vs. multi-male groups, depending upon factors such as the size and the defensibility of the female groups.

A concept which is central to all theories of mating system evolution is "defensibility" [or "defendability" as originally coined by Brown (1964)]. Defensibility refers to the ratio between the *benefits* of controlling a territory or group of females, (as measured by an increase in survival or reproductive success through enhanced access to resources or mates), and the *costs* of doing so, (as measured by time and energy spent in defense, and risks incurred as a result). We expect defense to be adaptive when the benefits exceed the costs. It is now generally accepted that *for a fixed cost*, the amount of resource or number of mates defended must be greater than some minimum value before benefits exceed costs, but also less than some maximum value at which competition is too low to warrant defense (Schoener, 1971; Carpenter and MacMillen, 1976). In other words, defense is most likely when the local density of resource or females is *intermediate* in value. As a corollary, the resource defended must be exploitable long enough, or the group of females suitably stable in composition, for the defender to obtain sufficient benefits. A defensible resource is thus one that is available for more than some minimum amount of time and which occurs within a limited range of local densities; a defensible group of females is one which is moderately stable in composition and within some limited range of group sizes.

It is also generally accepted that *for a fixed benefit*, the costs of defense increase with the area (or perimeter) to be patrolled and with the density of potential invaders (Holmes, 1970; Schoener, 1971; Gill and Wolf, 1975). Both defended area and invader densities are positively correlated with costs of defense. For a fixed ceiling on available time or energy for defense, it therefore follows that as invader density increases, the defender must reduce the size of the area defended. While this is generally so, there are exceptions which are critical to our discussion. In general, there are two types of territorial defense which can be distinguished in animals (Fretwell and Lucas, 1969; Fret-

well, 1972). Consider the common case in which territories are being established in a habitat with locally varying densities of some crucial resource. Suppose that potential settlers are relatively able to assess these local differences. Initially, all settlers will establish territories in the optimal portions of the habitat with each new invader forcing compression of the territories of earlier settlers. Eventually, further compression of existing territories in the best sites results in an invader obtaining less total resource than if he establishes a larger territory in a less rich site. Settlement then begins to occur in the next most optimal site and so on. As long as settlers and invaders are equally able to seize and hold territory, a "free" distribution of territories will result, in which territory size and local resource density are inversely related and all territories will contain the same *total* amount of resource. Free territorial distributions are apparently not uncommon in birds (Stenger, 1958; Cody and Cody, 1972a, b; Gargett, 1975). If, on the other hand, settlers are better able to defend territories than invaders can invade them, compression of territories in the better sites will halt at a lower settlement density than in the free case. Invaders will then be forced into the less rich sites earlier, and the total amount of resource in territories on the good sites will exceed that in territories on the poor sites. This unequal partitioning of resources is called a "despotic" distribution.

A despotic instead of a free distribution will arise whenever the costs to a defender of repelling each invader are not constant over all territory sizes, but instead decrease as territory size is compressed. It can also arise whenever, instead of holding the total amount of costs allocated for defense constant over all territory sizes, an animal is willing to increase these allocations as an inverse function of territory size. Despotic territorial distributions have been reported for a variety of bird species (Brown, 1969; Krebs, 1971; Klomp, 1972). In some of the cited examples, there is evidence that settlement at low invader densities is free, while that at higher densities is despotic. Some populations always experience high invader densities, typically show despotic behavior from the start, and exhibit "floater" sub-populations which are totally prevented from breeding by territorial holders.

The importance of the concept of defensibility in mating system evolution is easily demonstrated using the model of Verner (1964) as modified by Orians (1969) for the environmental determination of monogamy vs. polygyny. In this model, all males are presumed to adopt a strategy of defending a resource which a female requires. Orians then shows graphically that whenever the partitioning of the resources by territorial males is sufficiently unequal, females may do better to mate polygamously with an already mated male on a good territory than to mate monogamously with an unmated one on a poor territory. The model is interpreted by superposing a fixed grid of territories onto an underlying resource distribution. Where the resource is unevenly distributed in space, male territories will vary in contained resource, and polygyny can result; where the resource is more uniformly distributed, all male territories are similar and monogamy is the result. Following the suggestions of Verner and Willson (1966), Orians then notes that certain habitats, such as marshes, do show the expected correlation between high local variability in resource densities and the occurrence of polygyny.

While this model has had considerable popularity and success in some specific applications (e.g., Holm, 1973), its use as a predictor of mating systems is limited by the necessity to justify an implicit assumption. The nature of this assumption becomes clear when we note that the Orians model is really only a special case of the Fretwell and Lucas (1969) paradigm for territorial settlement. Seen in this way, monogamy is the result of male and female settlement histories which are similarly free or similarly despotic; polygyny is the result of the special case in which male settlement is *more* despotic than female settlement. More importantly, the presence of polygyny in one habitat and monogamy in another can only be predicted when we can also predict that male territorial settlement will be sufficiently more despotic in the first habitat. We are thus faced, in applying the Orians model, with identifying what makes one resource dispersion more defensible than another. The basic model circumvents this issue by taking the male distribution as a given, and showing how a subsequent "free" settlement pattern by females will result in monogamy or polygamy depending upon that initial male pattern.

The identification by Orians of marshes and other locally variable habitats as being particularly polygyny-prone is in fact an attempt to address the issue of site-specific defensibility. As noted above, the superposition of a fixed territorial grid onto a resource distribution will result in greater variance in the amount of resource per territory as the point-to-point variation in local resource density increases. If one assumes that a similarly sized grid is superimposed upon two habitats having the same total amount of resource but differing in local "patchiness", we could predict, using the model, that polygyny is more likely in the most patchy site. The problem is the assumption of similar territorial grids in the two contexts. When is it justified to assume that two species or two populations will have similar grid sizes? Why can invader males in the more patchy situation not force subdivision of the richer patches until all males have equal amounts of resource? The model thus only works if one assumes that both populations experience territorial compression down to some minimal value at which territorial defense becomes entirely despotic, *and* that this minimal value is similar for the two populations. The first assumption probably has considerable validity; the second is more likely when related species with similar morphologies and habits are being compared than when very divergent species are compared. We might even consider the possibility that two very divergent species have very different minimal territory sizes. Imposing the territorial grid of each on the same resource distribution would lead to polygamy in that with the larger grid size and monogamy in that with the smaller one. Thus either differences in grid size or differences in resource distribution could lead to differences in mating system.

We wish to formalize these comments as follows. Suppose that for a given species in a given habitat, there is a minimal territory size which has a mean value A . (A will vary somewhat in the population as a function of size, age, and experience of males; we shall just consider the average value). Suppose that males adopt a strategy of resource defense, and that females distribute themselves freely according to local abundances of resource. Let the average density of resource within the territory of male i be R_i . If a male has positioned

his territory over part or all of a rich patch of resource, R_i is large; if he settles over a less rich patch or between patches, R_i will be small. If B is the amount of resource required per female, then the number of females in the territory of male i is $(AR_i/B-1)$ if the male utilizes the resource, or (AR_i/B) if he does not. Note that a high variance in the numbers of females per male *among the males with females* is not a necessary consequence of the model. A large and uniform patch of resource might be settled by a few territorial males all with territory sizes of A and all with the same amount of defended resource. While these males would have similar harem sizes, partitioning is still despotic since other males have been excluded from the patch.

It follows that to use the Orians model, one is obliged to consider whether compression in the species being considered has reached a limiting value, and whether the A and B values are similar for the species or not. Where A and B are known to differ among species, it still may be possible to predict mating systems from R_i values if the differences in A and B only augment the differences in R_i . Where nothing is known about A or B , or where the degree of compression cannot be evaluated, the model will not be useful. Because unmated but mature males occur in all of the species we shall consider, it seems likely that compression to a critical and despotic level has occurred. We shall therefore presume that each of the populations discussed below is operating at its own value of A . We shall *not* presume without evidence that values of A and B are identical for different species. In general, one is obliged to estimate these values wherever possible. If a population is known to be despotic, (as evidenced by the existence of a floater population), an estimate of A for that population in that context is the average size of territories observed. Where food is the primary resource being defended, an index proportional to B is the body weight of females to the 3/4 power (McNab, 1963). Where these estimates are available, and where R_i values are known, it should be possible to determine which of two species is most likely to be polygynous or which is likely to have the larger harem size even though the absolute values of AR_i/B are not known. We shall be most concerned with the *maximal* values of R_i given a certain A and B since these set the upper limits on the numbers of mates that a male can have.

The preceding section identifies a set of specific variables which can be measured and used to predict whether males will be monogamous or polygynous given a resource-oriented strategy. It would seem obvious that we need a similar paradigm for female-defense strategies. Suppose again that competition results in compression of the area defensible by a male down to some critical value, A , at which further compression is unlikely. (Note that while area defensible is important in female defense, it is not the object of it. The difference is particularly important when males *dominate* as opposed to *exclude* other males in the group.) If the density of females within a male's defensible area is denoted by D_i , then the expected number of females per male will be AD_i . By analogy with the previous discussion, species having similar values of A will differ in mating system depending upon the values of D_i . The latter will differ depending upon the overall dispersion of females in the habitat. While female dispersion varies continuously, for convenience we recognize two general cases. In the

first, females are solitarily dispersed either to optimize foraging or to reduce predation through crypsis (Treisman, 1975a, b; Jarman, 1974). Female group size, which we denote by P , is 1. There are three sub-cases depending upon whether maximal values of AD_i are less than, equal to, or greater than one. $AD_i < 1$ is unlikely since males cannot breed under these circumstances. $AD_i = 1$ implies that males and females are similarly distributed and most likely live in monogamous pairs. It will occur whenever A or D_i or both are small. $AD_i > 1$ implies that the defended areas of males contain a number of solitary females. This "nested" system apparently occurs in a number of rodents, primates, and ungulates (Brown, 1966; Dubost, 1970; Charles-Dominique, 1972). When $P > 1$, the second general case, then females live in groups which move as units throughout the suitable habitat. Again we reject $AD_i < 1$ as unlikely. When $AD_i = 1$, then we expect to find groups which have equal numbers of males and females and most likely consist of monogamous pairs. An example appears to be the large rodent, *Dolichotis patagonum* (Genest and Dubost, 1974). When $AD_i > 1$, we may get several mating structures depending upon the relation between AD_i and P . If $AD_i = P$, we expect to find either one-male harems, as occur in zebras (Klingel, 1972) and Hamadryas baboons (Kummer, 1968), or multi-male troops with strong male reproductive dominance hierarchies as in savannah baboons (Hall and DeVore, 1965). In multi-male groups where one male does most of the mating, the presence of other males appears to be due either to the retention of male offspring (Eisenberg et al., 1972), or the need for cooperative multi-male defense when predators are common and large in size (Denham, 1971). If $AD_i < P$, then we expect several adult males to accompany the females and all to perform some of the mating. This occurs in a variety of large-sized African bovids (Jarman, 1974). We note that $AD_i < P$ either because the group of females is so large that it covers an area larger than A , or because even though P is small, the females occur at large individual distances and hence D_i is small.

We have now discussed the critical variables which must be measured to anticipate the mating forms *given* either resource-oriented or female-oriented male strategies. To complete a predictive theory of mating systems, we need to add two related components. The first is to identify those habitats and those habitat variables which predispose males to adopt either resource defense or female defense or neither. On the basis of our prior considerations, we presume that a habitat must meet the following three necessary conditions before a male should preferentially adopt resource defense: (1) resources are energetically defensible; (2) they are locally available for sufficiently long that a male can extract benefits; and (3) females and resources are so distributed that $AR_i/B > AD_i$. Similarly, a habitat will most likely lead to female defense if it meets the following three necessary conditions: (1) female groups or parts of groups are energetically defensible; (2) group size and/or composition are sufficiently stable for males to gain benefits; and (3) $AR_i/B < AD_i$ for all limiting resources. (When neither resources nor females are defensible, or when neither is sufficiently stable in time, we believe males are forced to adopt the "default" strategy of male mating aggregations. Evidence for this view will be presented in a subsequent publication). Correlations between habitats which meet one

set of conditions or another and male strategies will indicate whether the conditions are sufficient as well as necessary. The second task is to combine estimated values of A , B , R_i , D_i , and P to predict the final form of the mating system: monogamous pairs, permanent harems, multi-male groups with all males mating, multi-male groups with dominance, etc.

We cannot in this paper develop a general synopsis of mating systems and habitat contexts. Instead, we shall concentrate on the particular subset of species in which food constitutes the best defensible resource for males *and* in which female dispersion is determined primarily by food dispersion. In other words, we shall focus on species for which both R_i and D_i are direct functions of the food supply. This restriction appears to be satisfied for most of the African bovids recently reviewed by Jarman (1974). These animals appear to show male defense of either females or food supplies, and at least the upper limits on group size and group spacing can be predicted with confidence from knowledge of their food habits and food dispersions.

All antelopes tend to favor food sources which are high in protein relative to fiber content. Where diverse plant organs are available as food, antelopes will select those organs with highest protein contents; where diverse organs are not available, antelopes will seek out those plants whose phenology is at a stage (e.g., releafing, flowering, etc.), leading to high protein contents. These patterns are tied to habitats as follows. Species of antelopes which live in wet and stable forests encounter high plant species diversities and low seasonal synchrony in phenological activity. They thus can specialize both on specific organs and on particular stages of phenological activity. Their food is essentially "fine-grained" in dispersion: that is, it occurs in small patches of low richness, (measured in animals feedable), and both simultaneous and successively available patches occur at high densities (cf. Bradbury and Vehrencamp, 1976b for terminology). As Jarman (1974) has shown, such species tend to be socially "fine-grained" as well: that is, they occur in small groups and have small annual home ranges.

Antelopes in more seasonal habitats experience a rather different food dispersion. Typically, the vegetation consists of large patches of lower plant species diversity and greater local phenological synchrony than occurs in forest. Often the habitat consists of a mosaic of such large patches: hilltop and sumps in rolling catena, patches of trees separated by patches of grassland, etc. While patch size is generally larger than in forest, it varies from small clumps of bushes to enormous homogeneous expanses of grasses. Nearly all antelopes in such habitats show seasonal movements between patches of vegetation as they become seasonally active phenologically. However, the species differ in the frequency and in the range of these movements. Antelopes of intermediate size appear to be moderately specific about what plant parts are eaten, but less specific about the plant species and the degree of phenological activity. As a consequence of the latter two biases, they tend to remain within a given patch for longer and are more willing to move from one vegetation type into an adjacent but very different type than are larger bovids (Bell, 1970; Jarman, 1974). The ability to use adjacent patches in the mosaic and to remain longer on any given patch leads to lower annual home ranges than in larger species.

However, the high selectivity for plant parts reduces the effective richness of any patch and thus the number of animals it can support. As a result, group size and home ranges are intermediate for intermediately sized antelopes. Larger species appear to be more selective about mean phenological levels in the patches utilized, as well as vegetation types in which they forage. As a consequence, they move frequently from an exhausted patch of one type, bypass nearby patches of different vegetation types, and seek out newly active patches of the original type. They thus remain for less time in a given patch and travel long distances between successive patches. Home ranges are therefore large. In species such as wildebeest which specialize in grasses at a certain degree of growth, patch size is large enough that, even given some selectivity for grass parts, a patch can support a large group size. In others such as buffalo, which both eat grass and browse, patches may be smaller but the very low selectivity for plant parts facilitates the feeding of large groups. In short, food dispersion and as a result, social dispersion, both become more coarse with body size for antelopes in seasonal habitats (Jarman, 1974).

The mating systems for these antelopes are well known and appear to fall into categories which parallel the divisions according to social dispersion. Forest-dwelling species, nearly all of which are fine-grained socially, tend to live in monogamous pairs or have nested male-female territories (Jarman, 1974; G. Dubost, personal communication). Because females do not move between the territories of males, it is difficult to ascertain whether these males have adopted female defense or resource defense. In fact, when both R_i and D_i are determined by the same resource and are low in value, the two male strategies are effectively identical.

Antelopes in seasonal habitats show two trends, either or both of which could explain the patterns of male reproductive strategy. In general, as social grain becomes more coarse for seasonal habitat antelopes, the stability in the size of female groups increases (Jarman, 1974). It is not clear from Jarman's synopsis, or the work on which it is based, whether the correlation between social dispersion and size stability is due to a causal relation between group size and stability, one between the spacing of groups and stability, or one between some other ecological variable and both social dispersion and stability. Reasons can be imagined for any of these three relationships, but data to distinguish between them are apparently not available. Whatever the cause, the correlation implies that the conditions permitting female defense strategies will be increasingly met as social dispersion becomes more coarse. The second trend we have already noted: the duration of use of any given patch appears to decrease for species with coarser social dispersion (Bell, 1970; Jarman, 1974). This means that conditions permitting resource defense become increasingly unlikely as social dispersion becomes more coarse. Both of these trends lead to the same predictions: intermediately sized antelopes in seasonal habitats are more likely to adopt resource defense strategies than are larger species; larger species are more likely to adopt female defense. This is precisely what is found (Jarman, 1974). The dividing line appears to occur in wildebeest which adopt resource defense when sedentary, but show a hybrid strategy during migrations (Estes, 1969; Jarman, 1974).

Specific mating forms of antelopes are consistent with the criteria of earlier sections insofar as data are available. We have already noted that fine social dispersion tends to lead to monogamous pairs or nested territories. Antelopes of intermediate size in seasonal habitats show resource defense and hence temporary harems as females move between male territories. As one might expect, harem size for these species is directly correlated with the size of female groups and thus with social dispersion. It is not so well correlated with body size. This is partly due to a lack of an obvious pattern between values of A and body size even in sympatric species (cf. Estes, 1967; 1969). It is also due to the fact that while both R_i and B tend to increase with body size (Jarman, 1974), the ratio R_i/B may increase or decrease as a function of which variable increases *fastest*. Larger bovids generally adopt female defense. Most, such as buffalo, exhibit large groups with several reproductive males. The presence of several reproductive males implies that $AD_i < P$ for these animals. If this is so, it seems unlikely that it is due to a low value of D_i as this tends to increase with body size (Jarman, 1974). The most likely cause is a high value of P : when groups become sufficiently large, one male cannot control or exclude all other males. This interpretation is supported by the observation that Burchell's zebras, a sympatric herbivorous species showing frequent migrations between food patches, female defense, but much smaller groups, live in permanent one-male groups or harems (Klingel, 1972).

We now wish to summarize the preceding discussions into a single set of relations which can be tested in other mammalian species *given* that they meet the conditions of food determination of social dispersion and the availability of food as the only or optimal resource which is defensible. These relations are:

1. Fine-grained social dispersions, as occur in habitats with low seasonality and high food species diversity, generally lead to monogamous pairs or nested territories.

2. In seasonal habitats, compositional stability and duration of patch use appear to be inversely related. Where the former is high, female defense is favored over resource defense; where the latter is high, the reverse is true. Duration of patch use is determined by the habitat and the degree to which the animal's diet is specialized for certain seasonal conditions. Group stability may be determined by habitat features such as the temporal variance in the richness of successively available patches, by group size, by the dispersion of groups, or by some combination of these.

3. Where resource defense is favored, harem size depends upon the values of AR_i/B . While this generally increases with body size, social dispersion is a better predictor of observed values.

4. Where female defense is favored, the number of females controlled by a given male and the number of reproductive males per group depend upon the values of AD_i and P . As D_i increases, the number of females tended by a given male will go up as long as A also remains constant. While D_i and P seem positively correlated in antelopes, this may not be true in other mammalian groups, and even within antelopes, they may not change at identical rates. For a given A , the ratio of D_i to P will determine whether a group is a mobile harem or a multi-male group.

Results

In Table 1, we have summarized the pertinent data for an analysis of mating systems in five neotropical bat species: *Saccopteryx leptura*, *Peropteryx kappleri*, *Rhynchonycteris naso*, *Saccopteryx bilineata*, and *Balantiopteryx plicata*. For descriptions of study sites and methods of data collection, the reader is referred to our earlier papers (Bradbury and Vehrencamp, 1976a, b). In the latter of these papers, we presented evidence to support the conclusion that social dispersion in all of these bats is primarily determined by their food dispersions. We also showed that adult male members of most of the species exhibit defense of group foraging territories. We thus feel justified in using emballonurids to test the relations outlined above for African antelopes. For the test to be a good one, one would prefer that the bats showed enough similarities with antelopes to warrant contrasting them, but also showed enough differences in the covariances of the important ecological variables to further simplify the models by elimination of variables. In this regard, the bats do seem useful. They differ from the largely herbivorous antelopes by being entirely insecti-

Table 1. Mating systems and environmental data for five neotropical emballonurid bats

Variable	<i>S. leptura</i>	<i>P. kappleri</i>	<i>R. naso</i>	<i>S. bilineata</i>	<i>B. plicata</i>
A. Independent variables					
1. Social dispersion	Fine	Small groups	Mixed	Intermediate	Coarse
2. Group size	1-9	1-7	5-40	1-40	10-10 ³
3. Compositional variation	10-20%	Low	20-40%	80-100%	80-100% ^a
4. D_i on foraging grounds	Medium	Low	High	Low	Medium
5. A on foraging grounds (ha/male)	0.1-0.5	?	0.3-1.0	0.3-0.5	?
6. Index of R_i/B	29%	?	100%	36%	?
7. Patch use (weeks)	10+	?	2-6	8-10	?
8. Biomass density (grams/hectare)	14-97	6	34	6	7 ^a
9. Foraging habitat	Wet forest	Wet forest	Rivers	Seasonal forest	Seasonal savannah
B. Dependent variables					
1. Male strategy	Resource/female defense	Resource/female defense	Female defense	Resource defense	?
2. Mating form	Monogamous pairs	Monogamous pairs	Multi-male groups	Temporary harems	Mating swarms? ^a

See text for definition of variables and methods of computation

^a Data taken in part from Lopez-Forment (1976)

vorous. As a result, body weight and biomass densities are *inversely* related in the bats, a result exactly opposite to that in the antelopes. Similarly, while the dispersion of adjacent females tends to become reduced with body size in antelopes, adjacent female bats become more widely spaced as body size increases. Other differences will be noted below.

Several comments on computations and measures in Table 1 are necessary. Unlike our prior papers, the species are arranged by increasing coarseness of social dispersion and not body size. We have too few data on foraging in *P. kappleri* to estimate annual group foraging ranges. Because of its small group sizes, we have grouped it with *S. leptura*. *R. naso* have large groups but small annual ranges. This combination, for which there seems to be no obvious antelope analogue, does not fit easily along a gradient of increasing social dispersion coarseness. We shall call this combination a "mixed" social dispersion, and as with *P. kappleri*, we shall use group size as the criterion for ranking in the Table. Compositional variability is given as the average percentage change in group size per census. For *S. leptura*, *R. naso*, and *S. bilineata*, the values are based on equal numbers of censuses over an identical sample period and large numbers of groups. The value for *P. kappleri* is estimated from six censuses on four groups and that for *B. plicata* was computed from Lopez-Forment (1976) for five censuses on one group. Since we have previously argued that food and not roost space is the primary limiting resource for female emballonurids, (Bradbury and Vehrencamp, 1976b), we have given estimates of D_i for the foraging grounds only. These are given on an ordinal scale and are based upon the frequency with which each species was observed to practice female group foraging. Values of A are estimated from observed areas of male foraging territories. We cannot present absolute values of R_i/B , but have provided an index proportional to R_i/B . The index is computed by taking the measured average biomasses of aerial insects in a given species' foraging habitat and dividing that by the weight of females to the $3/4$ power. In comparing species, we are assuming that the constant of proportionality between metabolic needs and body weight to the $3/4$ power is identical for all emballonurids in the study. Since the index is highest for *R. naso*, we have normalized the values for the other species as a percentage of that peak value. Patch use durations are based upon the observed periods that marked bats remained over a given foraging site. Biomass densities for *S. leptura* are given as a range. This represents the values in Guanacaste, Costa Rica and Trinidad study sites respectively. The value for *P. kappleri* is possibly low since we cannot be sure all groups were located. That for *B. plicata* was computed by dividing the estimated number of bats roosting in Puerto Marquez, Mexico by the square of the most distant known foraging site (Lopez-Forment, 1976).

Discussion

The prediction from antelopes that socially fine-grained species should show monogamous pairs or nested male-female territories appears to be born out in the emballonurids. Since these expectations were derived more from consider-

ations of the small group sizes than from the closer spacing of groups, we have included *P. kappleri* with *S. leptura* in this category. Both species were found to occur as single adult pairs and recent young, or as small groups for which we have considerable evidence of subdivision into single pairs and young. It is instructive that both species are residents of wet and stable forests. While we have not argued that all wet forest species will have fine social dispersions, we have tried to show that fine social dispersions occur more frequently in these habitats than in others. The evidence here suggests that this correlation plus that between small groups and monogamy are relatively robust. Whereas Jarman (1974) suggests that smaller antelopes tend to be the forest species, there is no relation between body size and specialization for this habitat in emballonurids: *S. leptura* is one of the smallest species in our study while *P. kappleri* is the largest.

Of the remaining three species in the emballonurid study, the contrasts between *R. naso* and sympatric *S. bilineata* are particularly interesting. These two species have similar group sizes, but annual home ranges are much larger in *S. bilineata*. As with antelopes, there appears to be an inverse relation between the size stability of groups and the duration that a given foraging site is used. *R. naso* have moderately stable group sizes, but move foraging sites frequently; *S. bilineata* show much higher variability in group sizes over time, but tend to remain longer on a given patch of resource. We would thus expect the former species to show female defense more readily than resource defense and the latter species to show the converse. This appears to be the case. While adult male *R. naso* do defend a feeding territory, defense only appears to be directed against members of other groups. Although several males are usually present in such groups, they do not partition the group territory into exclusive subsections. On first appearance, it might seem that this is the case since the less resident male members and the adult but nonreproductive female members tend to space themselves out within the less used portions of the colony territory. However, the most resident male, which spends its time partially in patrolling inter-group boundaries and partly foraging with the mass of reproductive females, frequently invades the beats of the other males. It is especially significant that when the group-foraging reproductive females change feeding sites to an area within the usual beat of a less resident male, the most resident male attends them with no apparent interference from the other male members of the group. When the reproductive females return to the roost at night, the most resident male again follows them. In short, it seems clear that males in this species have adopted a pattern of female defense instead of resource defense.

In *S. bilineata*, the situation is quite different. Adult males *do* partition the current colony foraging patch into subsections. We have considerable evidence to show that the foraging territory of each male is defended not only against intrusion by members of other colonies, but also against intrusion by other adult males *in the same colony*. Females establish individual feeding beats within the foraging territories of particular males. When females change foraging sites, males do not attempt to follow them, but remain on their territories. This species thus appears to have adopted resource defense strategies.

The actual mating forms for these two species are generally consistent with expectations given the values of environmental variables. It is interesting that observed values of A for *S. leptura*, *R. naso*, and *S. bilineata* do not differ markedly. It is probable that the minimal defensible territory size is similar for most of the bats in this study. Number of females per male and number of reproductive males per colony will thus vary as a function of the values of D_i and R_i/B . One might expect that because female dispersion is determined by local food abundance, D_i values would be proportional to R_i/B values. While these two variables do covary in a significant way, D_i is at least in part dependent on the numbers of aerial insects as well. A site having a high R_i/B value might not always permit group foraging if this is due to a few very large biomass insects. In spite of this factor, Table 1 indicates that both D_i and R_i/B are higher for *R. naso* than they are for sympatric *S. bilineata*. We thus expect the former species to show a larger number of females per male than the latter. Unfortunately, while we have good data on harem size for *S. bilineata* in Trinidad and Guanacaste, we had many fewer *R. naso* groups which were sufficiently well marked to estimate female to male ratios. The available values, though not statistically significant, are in the right direction: mean harem size for 19 *S. bilineata* harems was 3.8 while the number of reproductive females in four *R. naso* groups having only one dominant male was 4.8. Because of lower values of R_i/B and D_i , each large colony of *S. bilineata* contains several adult males which mate with females. We might expect, given the patterns in antelopes, that as *R. naso* groups increase in size, eventually AD_i becomes less than P and several dominant males will be present. To date, we have not attempted to follow the very large groups of *R. naso* on the foraging grounds because of the difficulties in marking all members of the groups. The testing of the prediction and the determination of the value of P at which several dominant males are possible will be prime goals for subsequent studies on this species.

We have argued that *R. naso* have adopted female defense strategies while *S. bilineata* have adopted resource defense. Recent observations on mating in these species have raised some intriguing questions about problems peculiar to the latter strategy. It appears to be the case that most mating in emballonurids occurs at the day roosts (Bradbury and Emmons, 1974; Tannenbaum, 1975). For *R. naso* males, this poses no problems since they appear to follow the reproductive females as they fly from one site to another. For *S. bilineata* males, a difficulty arises since males are defending resources in one location (the foraging grounds), but can only profit from this activity at another (the day roost). It seems obvious that the only way males can gain from the defense of foraging areas is if they only admit those females to their nocturnal territories which also roost in their diurnal territories. While this correspondence is exactly what is found, how *S. bilineata* males might do this is totally unknown. One speculation which can be tested is that the elaborate vocal and olfactory exchanges between males and their current harem females at the roosts somehow enable a male to mark or identify the same females on the foraging grounds. As we have noted, these elaborate displays are absent from the repertoires of other species such as *R. naso* and *S. leptura*.

Unfortunately, elucidation of the mating system of *B. plicata* has failed

despite considerable effort by several field workers (Lopez-Forment, 1976; Bradbury and Vehrencamp, 1976a). It is extremely difficult to mark enough individuals in the large colonies of this species to determine whether either females or resources are regularly defended. It is clear from both studies that if males are defending resources, they are doing so only occasionally and for short periods. Most individuals in a given colony appear to use several foraging sites each night and to change foraging locations frequently during the year. Group size, as well, appears to be highly labile in this species. Some of this fluctuation is apparently due to differential habitat use and differential propensities to make seasonal migrations in the two sexes (Lopez-Forment, 1976). The available data thus suggest that *both* group stability and the duration of use of foraging sites are low in this species. These facts, plus the observations of increases in the proportions of males and in male calling activity in large colonies during the short annual copulation period, all suggest that male mating aggregations may be the most likely mating system for these bats. Seasonal mating "swarms" are known to occur in a variety of temperate insectivorous bats and seem to be associated with mating during periods of high populational flux (as the bats migrate to hibernacula), and dwindling levels of available food. These conditions are analogous to what we have outlined above for *B. plicata*. This prediction will become testable as we establish more completely marked populations of these bats.

It is worth summarizing the degree to which the antelope trends have or have not been confirmed in the emballonurid study. On the plus side, it does seem to be the case in both groups that fine social dispersions, and/or small groups, are primarily found in wet and stable forests and tend to consist of monogamous units. It also appears that in seasonal habitats, stability of group sizes and duration of patch use are inversely related, and this leads to predictable biases towards adoption of female or resource defense strategies. However, in *B. plicata*, this relation fails. Whether this is due to the much coarser social dispersion of this species or to its much more seasonal and arid habitat is not known. Lastly, where data are available, both the numbers of females per male and the numbers of reproductive males per group are directly related to values of A , D_i , R_i/B and P . On the debit side, it is not true, as it is in antelopes, that smaller-bodied species of bats tend to live in the more stable and diversified habitats. It is also not true that social dispersion becomes more coarse as a function of body size. The failure of this antelope correlation in the bats, even though the latter show a significant relation between local densities of insect prey and body size, is due to the fact that patch size is totally unrelated to body size. Thus patch richness, which is the product of local prey densities and patch size, and which determines group size, tends to have no relation to body size. Similarly, foraging ranges, which must be limited in part by the distance a bat can fly, are more dependent upon wing shapes than they are on body sizes at least within the studied species (Bradbury and Vehrencamp, 1976a). A final trend in antelopes is an increase in D_i as P increases. Again, because of the play-off in local prey densities and patch size in determining patch richness and group size, the correlation between these variables for bats is close to zero.

The differences noted above between the two groups do not contradict

the basic premise in both studies: that is, that social dispersion is primarily determined by the food supply and that selection for mating structures occurs within the bounds set by a given female dispersion. There is no evidence in either study that mating systems drive social dispersions. What *is* brought into question by the differences between the two groups of mammals is the notion that such simple variables as body size and habitat type will ever serve as good predictors of mating systems even within taxa having a similar dependence on a common resource. Instead, it appears that for each group of animals, field data must be provided to determine how the habitat is experienced by the different species. More specifically, one must know (1) the average size of resource patches; (2) the typical local densities of resource within an active patch; (3) how far an animal must travel between successively available patches and how long a given patch is used; (4) how consistent is the richness of successively available patches and what are the costs to an animal of changing groups when variation is high; and (5) the size of *A* for each species and whether settlement densities force compression to this value. Where two related species using the same or similar habitats show some divergence in resource preferences, any or all of the values of these parameters may differ and the two species can be expected to have different social dispersions and mating systems as a result. In short, there seem to be no short-cuts to direct measurement of resource dispersions if we wish to predict mating systems in mammals. However, once these are known, social dispersion ought to be predictable and mating systems derived as a result.

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