Effects of food resource distribution on the social system of Gunnison's prairie dog (Cynomys gunnisoni)

STEVEN E. TRAVIS AND C.N. SLOBODCHIKOFF
Department of Biological Sciences, Box 5640, Northern Arizona University, Flagstaff, AZ 86011, U.S.A.
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We tested the predictions of Slobodchikoff’s habitat variability — mating system model using the social system of Gunnison’s prairie dog (Cynomys gunnisoni). The model predicts that when resources are abundant and patchily distributed, social groups will include several females, while scarce, uniformly distributed resources will lead to smaller groups with single females. Gunnison’s prairie dogs form family groups consisting of a single adult male and female(s), and their young of the year, which occupy fixed spatial territories within a colonial framework. Resource abundances and distributions were characterized and compared at two colonies in northern Arizona. Resource abundance did not vary between colonies, while two separate measures showed resource distribution to be significantly more patchy at one colony than at the other. As predicted, there were significantly more territories with multiple females at the patchy colony, while single-female territories predominated at the uniform colony. The differences in resource abundance between colonies were not significant from a statistical standpoint. Sizable differences were observed, with the direction of the difference opposite to that predicted by the model.


Nous avons mis à l’épreuve les prédictions du modèle du système social en fonction de la variabilité dans l’habitat de Slobodchikoff dans le système social du Chien de prairie de Gunnison (Cynomys gunnisoni). Selon le modèle, lorsque les ressources sont abondantes et réparties de façon répandue, les groupes sociaux comprennent plusieurs femelles, alors que lorsque les ressources sont rares et réparties de façon uniforme, les groupes sociaux sont plus petits et comprennent une seule femelle. Les Chiens de prairie de Gunnison forment des groupes familiaux constitués d’un seul mâle adulte, d’une ou de plusieurs femelles et de leurs rejetons de l’année, et ces groupes occupent des espaces territoriaux fixes au sein d’une colonie. L’abondance des ressources et leur répartition ont été examinées et comparées chez deux colonies du nord de l’Arizona. L’abondance des ressources était semblable aux deux endroits, mais deux mesures prises pour évaluer la répartition des ressources ont révélé que cette répartition était significativement plus répandue chez l’une colonie que chez l’autre. Conformément aux prédictions, il y avait significativement plus de territoires occupés par plusieurs femelles chez la colonie où les ressources étaient moins réparties uniformément, alors que les territoires à une seule femelle présentaient que la colonie à ressources réparties uniformément. Les différences dans l’abondance des ressources entre les deux colonies n’étaient pas statistiquement significatives, mais il y avait cependant des différences appréciables dont le sens avait été opposé au sens théorique établi selon le modèle.

[Traduit par la rédaction]

Introduction

Behavioral ecologists have long sought to answer the question of why closely related species often differ in their propensities for group living, or sociality. A related and equally important area of inquiry attempts to ascertain the selective forces leading to the development of social systems that vary within species (see Lott (1984, 1991) for extensive reviews of this topic).

The resources hypothesis attempts to explain variation in social systems both within and between species. It suggests that social groups form and are maintained in response to those types of resource distribution most efficiently defended in a cooperative fashion (Crock 1965; Slobodchikoff 1984; Slobodchikoff and Shields 1988; Slobodchikoff and Schulz 1988). Single species that occupy environments with heterogeneous resource distributions are expected to display variable levels of sociality. Just as different species exploit different types of resources with different types of spatial distribution,

The habitat variability — mating system model of Slobodchikoff (1984) represents an attempt to describe the relationship between resources and sociality. It details not only the size of the social group, but also the form of the social system based on resource distribution and abundance. It makes the assumption that individual males will join together with several females to form a social group when resources are more efficiently defended in a cooperative fashion.

The primary goal of this investigation was to test the relationship between food resource variability and animal social systems. Slobodchikoff’s model predicts the propensity of animals to exist in single male/single female groups vs. single male/multifemale groups under circumstances of differing resource abundance and distribution. In this model, food resources are classified in terms of their abundance as either abundant or scarce, while food distributions are classified as either patchy or uniform. This results in four combined resource classifications: abundant and patchy, abundant and uniform, scarce and uniform, and scarce and patchy. The model predicts that resources that are abundant and patchy will lead to the development of social groups comprised of single adult males in association with two or more adult females, whereas resources that are scarce and uniform will lead to the development of groups consisting of single adult males in association with single adult females. The logic underlying these predictions is straightforward. Where resources are abundant and patchy, solitary males and females will be unable to defend enough patches to guarantee an adequate supply of resources, forcing them to group together for cooperation in resource
On the other hand, resources that are scarce and uniform will fail to supply adequate food for a group of more than two individuals, leading to high associations of single males and females. Uniform resources available in relative abundance should continue to favor the development of groups of no more than two individuals, since competition will incur a cost in the absence of a need for group defense of resources. Finally, scarce and patchy resources are expected to continue to support groups of more than two individuals, so long as resource abundance remains above some critical threshold, beyond which environmental constraints will come to preclude the occupation of a site by the species in question.

Gunnison's prairie dog (Cynomys gunnisoni), whose range is restricted to grasslands of the Colorado Plateau area (Hall and Kelson 1959), is particularly well suited for a test of the habitat variability - mating system model of Slobodchikoff (1984). The social system displayed by these animals has been described by Rayor (1988) and is very similar to that of the black-tailed prairie dog (Cynomys ludovicianus) which has been studied intensively by King (1955), and by Hoogland and his associates (Hoogland 1977, 1979a, 1979b, 1981a, 1981b, 1982, 1983a, 1983b, 1985, 1986, 1992; Foltz and Hoogland 1981, 1983; Garrett et al. 1982; Hoogland and Foltz 1982; Hoogland et al. 1989). Gunnison's prairie dogs display a social system which fits current definitions of highly social ground squirrel societies (Armitage 1981; Michener 1983). Colonial groups are organized into territories that generally contain one adult male, one or more adult females, non-breeding yearlings, and young of the year. Overlap between areas of use is high among members of the same territory and low between members of neighboring territories (Rayor 1988).

Prairie dog colonies are highly variable in terms of the plant food resources available, with patchy distributions prevailing on most, but not all, colonies (Shalaway 1976; Shalaway and Slobodchikoff 1988). This variation was shown to affect prairie dog group size during food provisioning experiments conducted previously (Slobodchikoff 1984).

In testing the predictions of the habitat variability - mating system model, the following specific questions were addressed: (i) Are patchily distributed and abundant plant food resources positively correlated with prairie dog group size? (ii) Are uniformly distributed and scarce plant food resources negatively correlated with prairie dog group size?

Methods

Two Gunnison's prairie dog colonies in northeastern Arizona were studied. Analyses of plant characteristics and prairie dog group composition were performed on 144-ha plots on each of the colonies during 1988 and 1989. The first study site, Antelope Hill (AH), was located west of the San Francisco Peaks on the edge of the Coconino National Forest, Coconino County, Arizona, at an elevation of 2348 m. The colony was in a meadow surrounded by ponderosa pine (Pinus ponderosa) forest. The second site, Potato Lake (PL), was located at the base of the northwestern slope of the San Francisco Peaks. 13 km northeast of Antelope Hill at an elevation of 2579 m. This colony was in a meadow surrounded by ponderosa pine forest, except to the southeast where aspen (Populus tremuloides) and Douglas-fir (Pseudotsuga menziesii) were the dominant species.

A determination of within-group group composition was made at each site during 1989 on the basis of locational data gathered for individual prairie dogs. As a system of reference, grids of surveyor's stakes spaced 10 m apart were established on each plot. Prairie dogs were live-trapped using Tomahawk squirrel-sized traps (0.50 x 0.20 x 0.20 m) 1 or 2 times per week from June through November of 1989, and from March through November of 1989. Locations of trapped animals were recorded, as were the locations of burrows entered by the prairie dogs following release from the capture site. In addition to having their sex, age-class, and reproductive status recorded at each trapping, all animals were marked with numbered metal ear tags on initial capture, and marked with black hair dyes for later visual identification. Body mass was measured while the prairie dog was suspended in a cloth sack from an Ohaus spring balance.

Further locational data were obtained through observations conducted once or twice per week. Two elevated viewing towers were constructed at each colony for this purpose. Over two study periods, a total of 112 h of behavioral observations were conducted at AH and 102 h at PL. Observations were evenly distributed throughout the active season. Because of difficulties in identifying animals obscured by vegetation, and the variable activity periods of individual prairie dogs, subjects were chosen for 6-min focal-animal sampling procedures (Altman 1974) in an opportunistic fashion. However, the choice of focal animal remained essentially random since obscuring vegetation was equally dispersed about the study plots, and daily activity periods did not differ significantly between individual prairie dogs. No single animal was ever included in more than one focal sample per standard 2-h observation period. Animal locations were recorded at the beginning and end of 6-min observation intervals, as well as immediately following major movements during foraging activities, and during social interactions. The nature of the interactions was also recorded.

Locational data on each animal, which consisted of X and Y grid coordinates for all trap locations, burrows entered, and behavioral observations, were subjected to a 50% Harmonic Mean Transformation with MCPAA 1.2 Home Range Analysis Software (National Zoological Park 1987). Home range values of 50% were chosen arbitrarily to establish core-use areas, since the prairie dogs may move through other territories in their foraging activities. This analysis was performed in order to identify the boundaries of each animal's primary activity area, which appeared to remain stable throughout the active season (no statistical evaluations were conducted to assess stability). Overlays of these boundary maps revealed broad areas of overlap among sets of individuals, allowing territory locations and their membership to be established. These results were then compared with the results of an average linkage cluster analysis performed with SPSS-X 3.0 statistical software (Nie et al. 1975). Cluster analysis is a multivariate technique that can be used to cluster animals into groups based on the Euclidean distances between their mean grid locations (calculated separately for X and Y coordinates). Associations of animals derived from cluster analyses were necessary for clarifying a limited number of associations that remained unresolved following the harmonic mean transformations, although in the majority of cases the two methods were in complete agreement.

The number of reproductive males relative to the number of reproductive females within a territory served as the basis for classification as a single adult (either male or female), a single male/single female, or a single male/multifemale grouping pattern. Reproductive status was judged from scrotal development in males and nipple development in females. For a territory to be classified as single adult, two criteria had to be met: only a single adult of either sex was present on the territory, and no juveniles were observed during the 1989 season. Single male/single female and single male/multifemale territories were occasionally seen to include more than a single adult male at PL, however, such groupings of males consisted of several philopatric yearling males sharing a territory with their mother and a single adult male judged to be of reproductive status. The retention of yearling males only at PL was apparently related to a significantly slower rate of maturation (measured as an increase in growth per day) among juvenile males at PL relative to AH during 1988, as determined via a t-test designed to compare differences in the slopes of regression lines (t = 16.6; df = 256; p < 0.001). Thus, we believe that there were no cases of more than a single reproductive male associating with the adult females) on a territory. Differences between
TABLE 1. Mean number of trapping events and focal samples per individual at Antelope Hill and Potato Lake

<table>
<thead>
<tr>
<th></th>
<th>Antelope Hill</th>
<th>Potato Lake</th>
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<tbody>
<tr>
<td></td>
<td>Trapped</td>
<td>Observed</td>
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<tr>
<td>1988</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juvenile</td>
<td>6.3</td>
<td>2.9</td>
</tr>
<tr>
<td>Adult</td>
<td>9.4</td>
<td>3.3</td>
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<tr>
<td>1989</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juvenile</td>
<td>4.6</td>
<td>3.2</td>
</tr>
<tr>
<td>Adult</td>
<td>12.0</td>
<td>8.0</td>
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Note: Values are given for each year of data collection and are split into adult and juvenile age classes.

the social systems predominating at the two sites were evaluated using a χ² contingency analysis. No assessment of social system type was possible before 1989, because of difficulties in distinguishing reproductive adults from nonreproductive yearlings.

Resource abundance was characterized within each study plot in terms of plant biomass. Biomass was measured during the height of the growing season (early to mid August) in 1989. Twenty 0.25-m² quadrats were chosen at random from within each study plot, and all aboveground vegetation was clipped, dried (in a drying oven), and weighed. Randomization was accomplished by tossing a 1 m diameter plastic hoop over the shoulder from a central location within each consecutive 30 × 90 m area of each study plot and allowing it to roll to a complete stop before census. Mean biomass was compared between sites via a one-way analysis of variance for a completely randomized design using BMDP4V statistical software (Dixon et al. 1983).

Resource distributions within study plots were measured in two ways: the first using within-site differences in biomass, and the second using Poisson variance-to-mean ratios of counts of food plants. Each study plot was divided into five equal area approximately 30 × 90 m in size, within each of which was located a single randomly located (see above) 1-m² quadrat sectioned into 0.25-m² squares. Quadrats were sampled for biomass (dry weight) and compared (within each colony) with the expectation that patchy resource distribution would result in statistically significant differences between quadrats, while uniform distributions would result in no such differences. This comparison was performed using a one-way analysis of variance for a completely randomized design (statistical software used was BMDP4V). Poisson variance-to-mean ratios were calculated from line intercept data gathered at each colony once per month from June through September 1988, and from May through September 1989. Resource distributions were compared using data from eight 90-m line transects laid out along every other grid column at each site. Line transects were sectioned into 15-m intervals for between-site comparisons, while within-site distributions in territories were compared by sectioning the line transects into 5-m intervals because of the relatively small size of territories (ca. 30 × 30 m). A count was then made of the number of occurrences of each plant species within each interval. Calculations were made of the mean number of occurrences and variance for 5–7 plant species at each colony. By dividing the variance for a given species by the mean, a value between zero and infinity was derived that provided a measure of the deviation of plant distributions from randomness, represented by a value of 1. Values of less than 1 were taken to represent uniformity, while values greater than 1 were taken to represent a clumped distribution (Zar 1984). Only those plant species whose use by Gunning's prairie dogs had been documented previously (Keeler 1939; Shalaway and Blobel 1988), or which the prairie dogs were observed ingesting during the study period, were included in this analysis. A mean was calculated for each colony for each month using individual Poisson variance-to-mean ratios weighted in terms of percent composition by species. This method of calculating a weighted mean was preferred over the alternative method of lumping all plant species during counts per interval, since the weighted mean method minimized the possibility of violating an important assumption of the Poisson distribution; that the probability of a count greater than zero for any interval is low (Zar 1984). Poisson ratios were averaged over all months within colony years for both between-site and between-social system comparisons.

Plant diversity was assessed at each colony to determine whether it was correlated with social system differences and should thus be considered as an additional factor potentially affecting prairie dog sociability. Counts of the number of individuals of each plant species censused during line transects were used as a means of comparing plant diversity between colonies, using all plant species present at each site. Between-site comparisons were made separately for each month of plant censusing during 1988 and 1989 to test the null hypothesis that diversities were equal at the two colonies. This analysis was performed on the basis of a t-test developed by Hutchinson (1970), which makes use of the Shannon index of diversity, $H'$.

Results

Social systems

Territorial associations at AH demonstrated a different pattern of sociality than those at PL, during 1989. The mean number of trapping events and focal samples upon which the determination of these associations was based are shown in Table 1. Single male/multifemale associations occurred significantly more often at AH than at PL ($χ^2 = 7.58; df = 2; p < 0.05$; Fig. 1). Of the eight territories at AH, five were occupied by one male and several females, and three were occupied by a single adult male and female. Of the 10 territories at PL, 1 was occupied by 1 male and several females, whereas 4 of the territories were occupied by a single adult male and female, 4 were occupied by only a single adult male, and 1 was occupied by only a single adult female. The number of adult females in multifemale groups was two or three.

The difference in group size between colonies did not appear to be related to differences in population densities, since adult densities (including yearlings) were similar at the two sites during 1989 (AH = 15.27 individuals/ha; PL = 20.14 individuals/ha; $χ^2 = 0.96; df = 1; p > 0.10$).
The nature and frequency of social interactions observed among prairie dogs during focal-animal sampling procedures indicated a trend toward greater involvement of females in territory defense at AH compared with PL. A total of 236 interactions were observed during 1988 and 1989 (149 at AH, and 87 at PL). Of these interactions, 194 were between members of the same territory, while 42 were between members of separate territories. The frequency of interterritory interactions considered to be of an agonistic nature (including displacements, chases, figts, and greet kisses followed by any of the above) was considered to be representative of the level of resource defense by territory members. At AH, males displayed agonistic behavior toward nonterritory members on four occasions, while females displayed such behavior on three occasions; these values were 15 for males and 1 for females at PL. A test for differences between colonies revealed a trend toward differing patterns of resource defense, with females contributing relatively less to defense than males at PL, relative to AH ($p = 0.07$; Fisher's exact test).

Sex ratios and reproductive outputs on the two study sites were compared in order to assess any relationship between these variables and group composition. Sex ratios did not differ between the two sites for either juveniles (AH = 18 male:16 female; PL = 6 male:9 female; $x^2 = 0.70, df = 1, n > 0.25$) or adults when combined with yearlings (AH = 7 male:15 female; PL = 16 male:13 female; $x^2 = 1.77, df = 1, n > 0.10$). However, since the adult ratio at AH showed a trend toward a female bias ($z = 1.49, p = 0.07$), whereas a 1:1 ratio prevailed at PL, sex ratios did reflect differences in the social systems between colonies.

Differences in female reproductive output were assessed both between colonies and between single male/single female vs. single male/multifemale territories. Territories that contained one adult male and at least one adult female that were known to have been in reproductive condition the year before, but which did not wean any young during the 1989 season, were excluded from the analysis reported here. The mean number of young produced per female per territory did not differ between AH (2.84 ± 0.49 (mean ± SE), range = 1.33 to 5.55) and PL (2.59 ± 0.42, range = 1.0 to 5.0) ($t = 1.10, df = 16, p > 0.20$). Nor did the mean number of young produced per female per territory differ significantly between single male/multifemale groups (2.39 ± 0.40, range = 1.33 to 5.55) and single male/single female groups (3.50 ± 0.75, range = 1.0 to 5.0) ($t = 1.64, df = 16, p > 0.10$). A separate analysis, which included adults known to be reproductively unsuccessful, yielded results similar to those reported here.

Resource abundance

Measurements of resource abundance showed that plant biomass did not differ significantly between the two colonies ($F = 1.48, df = 1, 38, p = 0.23$), although mean biomass was somewhat greater for PL (61.09 ± 18.02 g/m$^2$) than for AH (38.06 ± 5.87 g/m$^2$).

Resource distribution

Plant distribution differed between sites and between single male/single female vs. single male/multifemale territories, as revealed by both plant biomass and Poisson variance-to-mean ratios. Within-site differences in biomass between 1-m$^2$ quadrats were evident at AH ($F = 4.11, df = 4, 15, p = 0.02$), with mean measurements for 0.25-m$^2$ quadrat-squares ranging from 11 to 169 g on separate plots. These data provide clear evidence of a patchy distribution of plant resources at AH. Conversely, no significant difference was found at PL between plots randomly selected for quantification of plant biomass ($F = 2.30, df = 4, 15, p = 0.11$), suggesting a more uniform distribution than at AH. Mean biomass values ranged from 20 to 67 g at this site. Poisson variance-to-mean ratios calculated by colony and year provided further evidence of the difference in resource distribution between the two study sites. Ratios calculated from data gathered at AH were greater than 1.0 for both 1988 and 1989, demonstrating an uneven resource distribution, while those from PL revealed a more uniform distribution tending toward randomness, or a value of 1.0 (Fig. 2). As expected, Poisson variance-to-mean ratios were more representative of patchiness on single male/multifemale territories than on single male/single female territories (1.04 ± 0.05, Mann–Whitney $U = 32, n_1 = 3, n_2 = 7, p = 0.02$). In order to prevent group size differences from becoming confounded with colony differences in this comparison, a separate statistic was calculated using territories from AH alone. Similar results were obtained (single male/multifemale: 1.27 ± 0.05, single male/single female: 0.98 ± 0.07, Mann–Whitney $U = 15, n_1 = 3, n_2 = 5, p = 0.05$).
Plant diversity differed between colonies only during the early portion of each field season, prior to the onset of the summer rainy season in late June or early July (Table 2). Significantly greater levels of plant diversity were observed at AH compared with PL during June of 1988, and during May, June, and July of 1989. There were no statistically significant differences in plant diversity between colonies during the latter portion of each field season, as seen during July, August, and September of 1988, and during August and September of 1989.

Discussion

The results of this study demonstrate a correlation between resource distribution and Gunnison’s prairie dog social systems. According to the predictions of the habitat variability — mating system model of Stobodichoffik (1984), polygynous distributed and abundant resources should lead to the development of single male/multifemale associations, whereas uniformly distributed and scarce resources should be correlated with associations of single males and single females. The question of whether or not resource abundance is a necessary component of the model is difficult to answer in light of the current investigation, since abundances did not vary to a significant degree between study colonies. However, because differences in resource distribution affect sociality in the manner predicted, in spite of a lack of significant variation in resource abundance, and because a nonsignificant yet substantial difference in abundance demonstrated a greater availability of resources where they were the least patchy, the predictive value of the abundance component of the habitat variability — mating system model can, at least in part, be discounted.

The greater relative contribution to resource defense displayed by females at the primarily polygynous colony, AH, was suggestive of Stobodichoffik’s hypothesis (1984). The model predicts that polygyny will prevail only under circumstances that favor the defense of resources by groups of more than two individuals. These groups are assumed to consist of a single adult male together with several adult females, the latter assuming the primary role of defense. Conversely, monogamy is predicted to persist where much lower levels of defense are required, and under such circumstances males assume the role of territorial defense in order to prevent the incursion of rival males.

The apparent effects of resource distribution on the social system of Gunnison’s prairie dog are in keeping with the findings of a number of other studies examining ground squirrels and several other species of mammal. As stated by Stobodichoffik (1984), “the same relationship between resource quality and group formation also seems to hold true in the case of marmots (which are closely related to the prairie dogs).” Yellow-bellied marmots, *Marmota flaviventris*, have a variable social system (Armitage 1977), unlike the more solitary eastern woodchucks, *Marmota monax* (Barash 1974). The resource patches used by the yellow-bellied marmots are extremely variable (Andersen et al. 1976) and most territorial groups of yellow-bellied marmots are polygynous. The eastern woodchuck tends to live semicolonially in a more uniform habitat and is mostly monogamous (Merriam 1971). The Olympic and arctic marmots live in rather uniform, poor habitats in family groups of one male, two females, and the young. But, only one female bears young per year, so the system is functionally monogamous (Barash 1974). Furthermore, Jarman (1974) has documented a trend toward monogamy among species of African antelope utilizing distributed resources, and polygyny among species on more patchy resources. Finally, studies of polygyny within habitats and polygyny within patchy habitats (Clutton-Brock and Harvey 1977; Milton and May 1976; Siddiqi 1974), which is in keeping with the predictions of the habitat variability — mating system model.

The basic predictions of the habitat variability — mating system model are similar to those of several other models developed in an attempt to explain interspecific variation in social organization. These include the models of Verner and Willson (1966), Orians (1969), Emlen and Oring (1977), and Wrangham (1980, 1983). A consideration of these models in light of the findings reported here is necessary because genetically fixed differences in social organization among closely related species have presumably resulted from the progressive occupation of a variety of ecologically diverse habitats by several distinct populations of a single progenitor species. Thus, spatial heterogeneity in habitats occupied by a single species may lead to behavioral flexibility, allowing the persistence of several disparate social systems, which will become genetically fixed given sufficient time. While the test used in this study to evaluate the predictions of the Stobodichoffik model cannot be used to refute the predictions of these other models, each of them either differs in the basic assumptions it makes regarding the effects of resource variation on social systems, or provides the groundwork for models such as the habitat variability — mating system model, which relates specifically to particular species or contexts, e.g., species with strongly organized spatial systems.

The “Polygyny Threshold Model” of Verner and Willson (1966) and Orians (1969) assumes that groups of females will not “choose” to associate with a single male when they can raise more offspring by themselves while dwelling within the resource-rich territory of a polygynous male than they could with the aid of a monogamous male on a resource-poor territory. Implicit in this model is the assumption of habitat heterogeneity, and that females are mobile and can select which male to settle with. Thus, for differences in the mating system of a species to exist, so must differences in the quality of habitat available to those males establishing mating territories also exist. These tenets serve as basic assumptions of the habitat variability — mating system model of Stobodichoffik (1984), which assumes that social systems vary only under conditions of habitat heterogeneity and that females will always seek to maximize their fitness by joining only those territories that are most favorable in terms of potential fitness gains. However, Stobodichoffik’s model allows for additional predictions regarding those specific resource distributions that are most likely to favor the development of groups of two or more females.

The predictions of Emlen and Oring (1977), who propose that the “environmental potential for polygyny” will be highest where resources are patchy, are similar to those of Stobodichoffik (1984), however, they rely on the assumption of one territory being equivalent to one resource patch. The habitat variability — mating system model, on the other hand, assumes that polygyny develops because individual animals must defend several resource patches to insure an adequate supply of resources, and that such defense is only possible if animals group together. Thus, while resource patchiness is expected to lead to polygyny in both cases, Stobodichoffik’s (1984) model assumes that patchy environments consist of
many small patches, none of which is adequate to provide the necessary resources for all the members of a social group, while Emlen and Oring (1977) assume that a single patch is occupied by a single group.

The models of Wrangham (1980, 1983) assume that females form the core of the social group, as does the Slobodchikoff model, although these models vary in several key elements. Specifically, Wrangham's models predict that only related females will form groups, and that patch size will determine the mating system, whereas Slobodchikoff's model makes no assumptions regarding the relatedness of females and considers the synergistic effects that resource distribution and abundance have on social systems.

The effects of differences in levels of plant diversity at AH and PL during the early part of each active season must be considered as an alternative explanation for the observed differences in social systems between colonies. These differences temporally coincide with both the breeding and pre-weaning periods of Gunnison's prairie dog in Arizona, and could potentially affect the social dynamics of group formation, leading to differences in group structure. However, it is likely that the high plant diversity at AH, relative to PL, early in the season is a consequence of the higher prairie dog densities that typically prevail at AH at the end of each active season due to higher overall reproductive outputs. It has been shown previously that plant species diversity is increased on prairie dog towns relative to abandoned or adjacent sites that offer suitable habitat (Bishop and Lerwick 1976; Archer et al., 1984; S.E. Travis unpublished data). This evidence supports the role of prairie dogs as keystone species (Paine 1969) in many grassland communities. Clearly, then, the relationship between prairie dogs and plant diversity favors prairie dogs as the controlling agent, and not vice versa.

A competing hypothesis that has not been considered in this paper is the predator hypothesis. This hypothesis (see Hoogland 1977, 1979a, 1981a) proposes that group size (either within a territory or within a colony) should increase directly with the threat of predation, especially since prairie dogs benefit from predator information in the form of alarm calls gained from conspecifics (Slobodchikoff and Coast 1980; Slobodchikoff et al., 1986, 1991). Evidence contrary to this hypothesis has been obtained in a study conducted concurrently with the one reported here, and will be considered elsewhere.

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