

Gunnison's prairie dog (*Cynomys gunnisoni*): testing the resource dispersion hypothesis

J. L. Verdolin

Received: 7 January 2008 / Revised: 9 January 2009 / Accepted: 12 January 2009 / Published online: 12 February 2009
© Springer-Verlag 2009

Abstract Few studies have experimentally tested the resource dispersion hypothesis (RDH). In this study, I tested whether space use and social organization of Gunnison's prairie dog responded to changes in the dispersion and abundance of resources. Food manipulations were carried out during the reproductive and nonreproductive seasons across 2 years. Gunnison's prairie dog adults responded to the experiments by decreasing territory size as food became patchier in space and time. Both males and females modified their home ranges, with no detectable difference between sexes, either prior to or during the experiments. As food became patchier in space and time, the spatial overlap of adults increased, whereas it decreased as food became more evenly dispersed. The average size of a group, defined as those individuals occupying the same territory, did not change significantly as a result of the experiments. Where changes in the composition and size of groups did occur, there was no indication that such changes were sex specific. Results from this study support critical components of the RDH and strongly suggest that patterns of space use and social structure in Gunnison's prairie dogs are the result of individual responses to resource abundance and distribution.

Keywords *Cynomys gunnisoni* · Resource dispersion · Social structure · Group living

Introduction

A general principle, first described by Crook (1965), is that individuals in a population tend to aggregate more as the dispersion of their food becomes more clumped (patchy) in space. This broad correlation has been verified in an extensive array of organisms (birds: Myers et al. 1981; Stouffer et al. 1988; Gunnison's prairie dogs, *Cynomys gunnisoni*: Slobodchikoff 1984; Travis and Slobodchikoff 1993; European badgers, *Meles meles*: Kruuk and Parish 1982, 1987; brown hyenas, *Hyaena brunnea*: Owens and Owens 1996; primates: Yamagiwa and Hill 1998; see Lott 1991 for review). Many of these correlations are likely due to the costs associated with competition among group members for resources balanced against the benefit of exploiting a clumped resource (Waser 1977, 1988; Bradbury and Vehrencamp 1976; Janson 1992; van Schaik and Janson 2000).

An extension of this general pattern, the “resource dispersion hypothesis” (RDH) states that the abundance and distribution pattern of critical resources may provide a distinct underlying mechanism for the evolution of groups (Macdonald 1983, 1984; Slobodchikoff 1984; Carr and Macdonald 1986; Slobodchikoff and Schultz 1988; Bacon et al. 1991a, b; da Silva et al. 1993; Woodroffe and Macdonald 2000). The RDH differs from Crook's hypothesis in that it is limited to territorial animals, while Crook suggested that territoriality could act as an impediment to sociality (Crook 1965). Although the RDH is also similar to Brown's (1982) model of optimal group size, two unique assumptions differentiate the RDH from this and other models. First, the RDH assumes shared territorial defense as the primary benefit to group living. Second, no other benefits or external forces are assumed necessary to explain group formation and maintenance, though the model does not preclude other benefits from existing.

Communicated by P. Banks

J. L. Verdolin (✉)
Department of Ecology and Evolution, Stony Brook University,
Stony Brook, NY, USA
e-mail: jlverdolin@life.bio.sunysb.edu

The RDH can also be thought of as an alternative hypothesis to grouping patterns that reflect more typical male mammalian mating strategies. Much of the research on mating systems has centered on the prediction that males and females respond to different selection pressures. Female distribution is predicted to follow the distribution of resources and predation risk, whereas male distribution will be primarily determined by the spatial and temporal availability of females rather than of resources (Emlen and Oring 1977). Thus, it is possible that females only follow RDH, whereas males follow individual mating strategies but are not involved in resource defense against other groups (Waser 1977; Packer et al. 1990). Alternatively, if resources are the dominant influence on aggregation patterns, variation should be the result of the changes in the grouping behavior of both males and females, while remaining independent of any particular mating strategies.

The RDH has been criticized as an untestable hypothesis because of a lack of well-defined predictions (Von Shantz 1984). As a result, its application as a mechanism for the evolution of group living has been limited. More recently, theoretical work has focused on identifying the RDH predictions, thus creating a framework for examining animal grouping patterns (Bacon et al. 1991a, b; Johnson et al. 2002). There are two characteristics of resources that are suggested to play a role in grouping behavior: (1) their abundance or richness and (2) their distribution or dispersion in space and time. Like other models, the formal RDH broadly predicts that the abundance of resources constrains group size, but, in contrast, RDH predicts that the spatial dispersion, or patchiness, of those resources directly influences territory and home range size. In addition, temporal fluctuations in resource abundance and distribution may create stochastic changes in the environment that could affect aggregation patterns and spatial organization of individuals (Maher and Lott 2000; Johnson et al. 2002). Under the RDH, the expectation is that, as resources become more variable in space and time (more heterogeneous), territory size would increase because of the need to defend larger areas that consistently contain enough food patches to satisfy even a single animal. In addition, such food patches may be productive enough, once located, to support several individuals, so the defense of a larger territory may favor larger group sizes.

Although many species show patterns of correlations consistent with the RDH, more rigorous experimental studies are scarce due to practical difficulties in testing the RDH in natural populations. Though not specifically testing RDH, some experimental evidence does exist to suggest that resource abundance and distribution may exert a strong influence on aggregation patterns. For example, by manipulating food abundance and dispersion simultaneously, Sánchez-Prieto et al. (2004) found that group size increased

in Iberian red deer when food was patchier and denser. In addition, Davies and Hartley (1996) demonstrated that territory size increased with increasing food patchiness in dunnocks. Though neither study system meets the assumptions for testing the RDH, both studies indicate that behavioral flexibility in response to changing environmental conditions may be common.

Gunnison's prairie dogs (*C. gunnisoni*) provide an excellent model system for experimentally testing the RDH and satisfy the assumptions associated with this model in the following ways. First, all individuals within a territory have access to all parts of the territory, and both males and females communally defend territories larger than individual home ranges (Rayor 1988; Verdolin 2007). Second, food resources are heterogeneous and individuals respond to this variation (Slobodchikoff 1984; Travis and Slobodchikoff 1993). Third, there is observational and experimental evidence suggesting that the social structure associated within a territory varies with the availability and distribution of food resources (Slobodchikoff 1984; Travis and Slobodchikoff 1993; Travis et al. 1995). Lastly, although previous research suggests that female kin-related groups form the core social unit in this species (Hoogland 1999), data from these populations indicate that kinship benefits are not driving social patterns (Verdolin and Slobodchikoff 2009).

In this study, I explored the effect of resource abundance and dispersion on Gunnison's prairie dog social organization and space use through a series of food manipulations testing eight specific predictions of the RDH (Table 1). Predictions 1–4 were derived from Johnson et al. (2002), while the remaining predictions naturally emerge from RDH, though they are not explicitly expressed in the formal model. It should be noted that the model indicates that predictions 2–4 depend on initial conditions (Johnson et al. 2002). However, because specific directional predictions

Table 1 List of predictions related to the hypotheses tested in this study, most of which (1–4) were specifically derived from Johnson et al. (2002)

Variable	Predictions
1. Resource abundance	+ Correlation with GS
2. Resource dispersion even	- Correlation with GS and TS
3. Resource dispersion patchy	+ Correlation with GS and TS
4. Resource dispersion spatially temporally heterogeneous	+ Correlation with GS and TS
5. Resource dispersion even	- Correlation with HRO
6. Resource dispersion patchy	+ Correlation with HRO
7. Resource dispersion spatially temporally heterogeneous	+ Correlation with HRO
8. Sex	No difference
9. Season	No difference

GS group size, TS territory size, HRO home range overlap

depending on initial conditions are not available, this study is testing the hypotheses only as presented in Table 1.

Materials and methods

Study area

Two colonies of Gunnison's prairie dogs were studied in northern Arizona from May 2003 to August 2005. The first study site, Humane Society (HS), was established in May 2003. The second study site, Country Club (CC), was established in August 2003. Experimental manipulations of resource abundance and distribution were conducted from June 1, 2004 to August 1, 2004 and April 1, 2005 to May 6, 2005. Data from 2003 are excluded from the current analysis.

Both colonies were located within the city limits of Flagstaff, AZ, USA. Within each study site, two 1-ha plots were created. At both sites, the location of the plots (HS I, HS II, CC I, and CCII) was separated by a distance of 0.2 km and a road. With the exception of one individual who moved in August 2004 from HS I to HS II and two individuals from CC I that moved to the boundary of CC II, individuals in different plots did not physically interact with one another or occupy the same area at any time during this study. For each plot, at both HS and CC, a $100 \times 100\text{-m}$ letter/number grid system consisting of 100 $10 \times 10\text{-m}$ quadrats was established using surveyor stakes.

I assigned individuals to social groups and determined group territory boundaries using data on animal locations collected during live trapping and behavioral observations as described in Verdolin (2007). An intrusion refers to an event where an individual not belonging to the social group entered the territory and was aggressively chased out of the territory. The number of social groups and territories occurring on each plot is listed in Table 2.

The abundance and distribution of food plants were obtained by monthly sampling of all plots from April to August each year. A detailed description of methods used for assessing percent cover and estimating aboveground biomass is provided in Verdolin (2007). Briefly, percent

cover was estimated for all plots and all territories within each plot, from digital images using Optimas 3.0. Available aboveground biomass for each plot was estimated using the average dry weight of 100-cm^2 food plant samples collected from 15 randomly selected 100-m^2 quadrats each year. Territory food patchiness during the nonexperimental portion of the study was calculated as the variance to mean ratio of biomass per square meter or index of dispersion (Krebs 1999). Territory food patchiness during the experiments was also calculated as the index of dispersion, with the daily amount of sunflower seeds distributed to each territory incorporated in the mean biomass per square meter. Changes in patchiness were calculated as the difference in patchiness prior to and during the experiments. In 2005, just prior to the onset of the experiments, there was little aboveground vegetation cover. Individuals were observed foraging on roots and were likely living off of post-hibernation fat reserves. Due to the lack of aboveground biomass in March and widespread snow cover, data to estimate pre-treatment patchiness were unavailable. Instead, a pre-treatment patchiness of 1 was assigned to all territories, corresponding to a random distribution.

All home ranges and territory areas were calculated using the fixed kernel density estimator. When using the fixed kernel approach with a level of smoothing selected by least squares cross-validation, results are less biased and more appropriate for nonnormal distributions (Worton 1995; Seaman and Powell 1996). As opposed to the adaptive kernel, the fixed kernel approach is more stable for probability contours exceeding 80%. Seaman et al. (1999) suggest that contours greater than 85% do not provide meaningful biological information and are less reliable. Therefore, I used only the 85% contour probabilities for all individual home ranges, territory areas, spatial overlap of individual home ranges, and all statistical comparisons (see Verdolin 2007 for details). The proportion of the total home range that any one target individual overlapped with another individual was calculated by taking the area overlapped divided by the home range of the target individual. Proportions were arcsine-transformed for analysis. Changes in home range overlap were calculated as the difference between the proportion of overlap between two individuals prior to the experiments and the proportion of overlap during the experiments.

Experimental design

Food manipulation experiments were conducted by imposing a spatiotemporally even treatment, a spatially patchy treatment, or a spatiotemporally heterogeneous treatment in 2004 to the study plots. In 2005, the experiments were repeated using only the even and spatiotemporally heterogeneous treatments. The food source used was sunflower seeds, a

Table 2 Experimental design for the post-reproductive season in 2004 and the reproductive season in 2005

Plot	2004 Experiments	2005 Experiments
CCI	Patchy (6)	Heterogeneous (4)
CCII	Control (4)	Control (5)
HIS	Heterogeneous (5)	Even (4)
HSII	Even (5)	—

The number of social groups/territories occurring on each plot is in parentheses

high-energy naturally occurring food source. Prairie dogs within each plot were supplemented with 70% of their daily energetic requirements. The average weight of a sunflower seed used in this study is 0.065 ± 0.003 g, $N=15$ (unhusked), and 0.040 ± 0.002 g, $N=15$ (husked). The estimated energetic requirements for an adult prairie dog weighing an average of 836.8 ± 26.15 g ($N=36$) is 660.22 ± 4.71 kJ/day (Nagy et al. 1999). Thus, the estimated daily food intake per adult prairie dog, based on 16.9 kJ/g of dry matter for granivores, was 39.06 ± 3.59 g, yielding a value of 44.0 g of unhusked sunflower seeds per individual in order to supplement 70% of the daily energetic requirement.

Post-reproductive season experiments

Food manipulations during the nonreproductive season began on June 3, 2004 and continued until August 1, 2004. This time period encompassed the start of juvenile emergence (early June) and the start of the rainy season (mid-July). One of the four plots, selected at random among the four, served as the control. Each of remaining three plots received one of the other treatments, according to a fixed rule. The plot with the highest natural food patchiness received the even treatment; the plot with the least natural food patchiness relative to the other experimental plots received the patchy treatment and the experimental plot with an intermediate patchiness received the spatiotemporally heterogeneous treatment (Table 2).

An even distribution was obtained by dividing the total amount of seeds by 100 and each 10×10 -m quadrat received equal portions every day. The portion distributed in each quadrat was spread as uniformly as possible to minimize the creation of mini-patches. To achieve a higher spatial patchiness, ten 10×10 -m quadrats were selected using a random number generator in Excel. The total amount of sunflower seeds to be distributed daily was divided by 10 and each selected quadrat received that amount daily throughout the duration of the experiment. The portion distributed to the ten patches was placed in the center of each quadrat. As resources can vary temporally as well as spatially, the plot with the intermediate patchiness value (relative to the others) was given a spatiotemporally heterogeneous treatment. Again, ten 10×10 -m quadrats were selected at random and the total amount of sunflower seeds to be distributed daily was then divided by 10 and placed in the center of each quadrat. Each selected quadrat received that amount for 2 weeks. After 2 weeks, an additional set of ten quadrats were selected at random and food was distributed in the new set of quadrats for 2 weeks. This process was repeated four times throughout the experiment. Territories did not necessarily receive equal amounts of food because the size of a territory and the fraction of its area included in the hectare plot affected how

much food it received, in addition to the random choice of locations to receive supplements. However, the variation in food added per territory was similar for all three experimental treatments (Bartlett's test, $P=0.267$).

Reproductive season experiments

Extensive flooding during the winter of 2004 resulted in 100% mortality of all individuals on HS II, eliminating this plot from the study in 2005. Food manipulations during the mating portion of the reproductive period began on April 2, 2005 and continued until May 11, 2005. The CCII remained the control plot, while HS I received the even treatment and CC I received the spatiotemporally heterogeneous treatment (Table 2). The procedures were identical to the post-reproductive season experiments. Though territories did not receive equal amounts of food, the variation in food added per territory was similar for all three experimental treatments (Bartlett's test, $P=0.149$).

Statistical analysis

Previous results indicated that yearlings and adults had different home range sizes and that yearling home range overlaps did not correlate with differences in food patchiness (Verdolin 2007); thus, all analyses of home range and food patchiness were conducted on adults. Because it is not possible to reliably distinguish between adults and yearlings by weight (Tileston and Lechleitner 1966), all males and females of unknown age were classified as adults. Previous results during the nonexperimental portion of this study also indicated that territory size predicted the number of individuals in a group, regardless of age and sex (Verdolin 2007); therefore, analyses of group size include both male and female adults and yearlings.

Aboveground vegetation was recorded monthly and analyzed to calculate territory food patchiness. Due to the monthly sampling regime, there could have been a complex correlation structure among the sequential sampling periods for a given colony, requiring the use of repeated-measures analysis of variance (ANOVA). However, repeated-measures ANOVA is not required when sequential data points within a category share a common covariance structure across categories (SAS Institute 2000). A test for sphericity was used to test this assumption for patchiness of food within colonies across months. The results were not significant for each colony in each year (2004: $X^2=3.70$, $df=4$, $P=0.595$; 2005: $X^2=0.56$, $df=4$, $P=0.762$). Therefore, I accepted the null hypothesis that different months shared the same covariance structures across time. This criterion then allowed me to use univariate analyses for the reproductive (April–May) and post-reproductive (June–August) experimental periods.

I used a general linear model (GLM), except where the dependent variable had a Poisson distribution, in which case I used a generalized linear model (GdLM). Average food patchiness for each period was used to test the effect of patchiness of food on the spatial overlap of individual home ranges. Biomass per square meter and territory size were log-transformed to reduce heteroscedasticity. Arcsine transformation was performed on the proportion overlap of individual home ranges. Year, site, and interaction terms are not reported, except where significant. Statistical analyses were performed using JMP 4.0 and Statistica software, and all P values reported are two-tailed.

Results

Post-reproductive season (2004)

Adult males and females did not differ in their responses to the experiment. A two-way ANOVA found a main effect on changes in home range as a result of the treatments ($F_{3, 58} = 4.75, P=0.005$). There was no main effect of sex on changes in home range ($F_{1, 58} = 0.72, P=0.399$), nor was there any interaction effect between sex and treatment ($F_{3, 58} = 1.26, P=0.297$). In addition, the starting number of males and females did not explain changes in either the number of males added or lost to a group (GLM: whole model: $R^2 = 0.06, F_{2, 17} = 0.55, P=0.669$) or the number of females added or lost to a group (GLM: whole model: $R^2 = 0.22, F_{2, 17} = 2.45, P=0.116$).

Prior to beginning the food manipulation experiments in 2004, log territory size was a significant predictor of group size (GLM: whole model: $R^2 = 0.61, F_{1, 18} = 28.36, P<0.001$). Log mean food biomass per square meter increased with log territory size (GLM: whole model: $R^2 = 0.29, F_{1, 18} = 7.18, P<0.015$) and the log food biomass per individual increased with log territory size (GLM: whole model: $R^2 = 0.42, F_{1, 18} = 12.82, P<0.001$) suggesting that larger territories were more productive. In addition, the per capita number of intrusions did not depend on group size (GdLM: $W = 0.04, P = 0.854, N = 20$). While group sizes changed on most territories during the experiment (Table 3), mean group size per treatment plot did not change significantly (Wilcoxon paired signed rank test: $W = 4, P = 0.920$). Although treatment type did not strongly affect group size after the experiments, the positive relationship between group size and territory size remained significant (GLM: whole model: $R^2 = 0.47, F_{4, 15} = 3.45, P = 0.033$).

There was a significant treatment effect on the change in territory size (ANOVA: $R^2 = 0.59, F_{3, 16} = 7.65, P<0.002$). Territories on plots receiving the patchy and heterogeneous food treatments decreased in size, while territories on the even plot increased in size to about the same extent as those

Table 3 Changes in group size (GS), for each territory by experimental treatment in 2004 and 2005

Plot	Treatment	2004	Territory	GS	Treatment	2005	Territory	GS
CCII	Control	1	1	Control		1	-2	
		2	0			2	0	
		3	-2			3	1	
		4	1			4	1	
CCI	Patchy	1	-2	Spatiotemporally		5	0	
		2	-1	heterogeneous		1	0	
		3	-4			2	0	
		4	-3			3	-1	
		5	1			4	-5	
		6	0			5	-	
HIS	Spatiotemporally Heterogeneous	1	1	Even		1	-2	
		2	1			2	0	
		3	0			3	0	
		4	3			4	0	
HSII	Even	5	0					
		1	0					
		2	3					
		3	-					
		4	1					
		5	1					

on the control plot (Fig. 1a). A *post hoc* comparison of treatment means to the control, using Dunnett's test, indicated that the patchy and spatially heterogeneous plot, but not the even plot, were significantly different from the control at $P=0.05$. Prior to the experiments, there was no significant relationship between food patchiness and territory size (GLM: whole model: $R^2 = 0.05, F_{1, 18} = 1.02, P = 0.325$). However, the change in food patchiness was significantly correlated with the changes in territory size during the experiment (GLM: whole model: $R^2 = 0.45, F_{1, 18} = 14.74, P<0.001$). Changes in territory size on the even plot followed a similar pattern to the control plot. A comparison of territory sizes measured at 2-week intervals, beginning 2 weeks after the start of the experiments, showed that the territories on the even plot expanded significantly more than those on the control plot (t test: $t_7 = -2.909, P=0.023$). This difference in expansion pattern was no longer significant after the rainy season began (paired t test: $t_7 = -2.232, P = 0.061$), suggesting that the effect of the experiments were diluted as the summer progressed, as natural foods became more common and palatable.

There was a significant treatment effect on the change in mean adult home range overlap (Fig. 2a; ANOVA: $R^2 = 0.62, F_{3, 14} = 7.47, P=0.003$), with home range overlaps on plots receiving the patchy and heterogeneous food treatments increasing, whereas the mean home range overlap for territories on the even plot decreased and was more similar to that of the control plot. A *post hoc* comparison by Dunnett's test also indicated that the patchy and spatially heterogeneous plots, but not the even plot, were signifi-

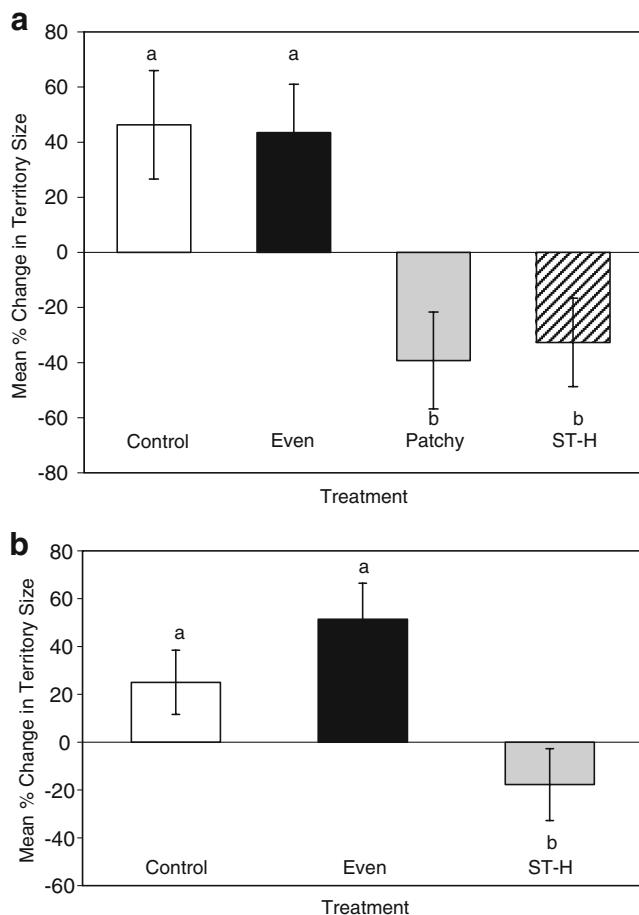


Fig. 1 Mean (\pm SE) percent change in territory size by food dispersion treatment type in the nonreproductive season (2004) and reproductive season (2005). **a** During the nonreproductive season, territory sizes changed significantly as a result of the food dispersion treatment, with territories on the patchy and spatiotemporal heterogeneous (ST-H) plots increasing and territories on the even and control plots decreasing. **b** During the reproductive season, territory sizes again changed significantly as a result of the food dispersion treatment, with territories on spatially temporal heterogeneous plot increasing and territories on the even and control plots decreasing. Treatments marked *a* were similar to each other but significantly different from those marked *b*. The difference in territory size was the dependent variable used in the statistical test

cantly different from the control at $P=0.05$. The difference in territory patchiness was significantly correlated with the change in mean adult home range overlaps (GLM: whole model: $R^2=0.38$, $F_{1, 11}=6.23$, $P=0.030$).

Reproductive season (2005)

As in 2004, adult males and females did not differ in their responses to the experiment. A two-way ANOVA found no significant main effect on changes in home range size due to sex ($F_{1, 31}=0.36$, $P=0.499$) or to treatment ($F_{2, 31}=1.90$, $P=0.133$) and no interaction between sex and treatment ($F_{2, 31}=1.42$, $P=0.272$). In addition, the starting number of

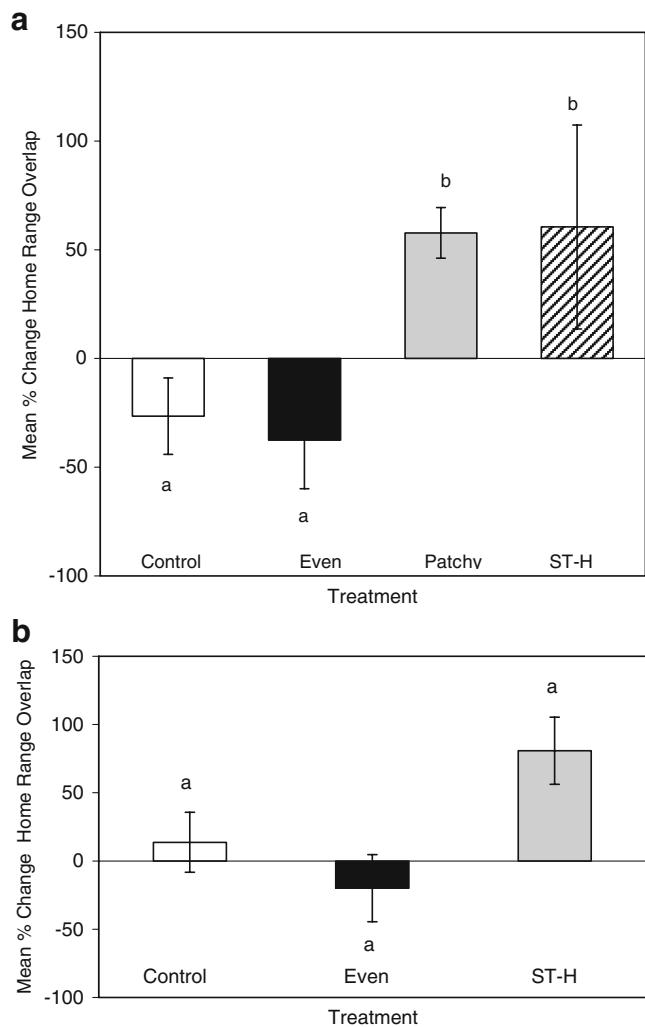


Fig. 2 Mean (\pm SE) percent change in adult home range overlap by food dispersion treatment type during the nonreproductive season (2004) and reproductive season (2005). **a** During the nonreproductive season, home range overlap changed significantly as a result of the food dispersion treatment. The mean change in home range overlap showed a decrease on the patchy and spatiotemporal heterogeneous (ST-H) plots and an increase on the even and control plots. **b** During the reproductive season, the mean change in home overlap as a result of food dispersion treatment was significant, with the mean difference increasing on the spatiotemporal heterogeneous plot and decreasing on the even and control plots. Treatments marked *a* were similar to each other but significantly different from those marked *b*. Difference in adult home range overlap was the dependent variable used in the statistical test

males and females did not explain changes in the number of males added or lost to a group (GLM: whole model: $R^2=0.45$, $F_{2, 11}=3.67$, $P=0.066$). Similarly, the starting number of males and females did not explain changes in the number of females added or lost to a group (GLM: whole model: $R^2=0.14$, $F_{2, 11}=0.73$, $P=0.765$).

Log territory size was again a significant predictor of group size prior to the experiments (GLM: whole model: $R^2=0.38$, $F_{1, 12}=6.76$, $P=0.024$). Food biomass was not

analyzed in 2005, as measurements of biomass were not feasible in March, prior to the experimental treatment (see “Materials and methods”). Although group sizes changed, both increasing and decreasing (Table 3), mean group size did not change significantly with treatment (Wilcoxon paired signed rank test: $W=24$, $P=0.106$). One territory on CCI contributed heavily to the changes in group size. Shortly after the experiments began, five individuals left this territory, with four individuals, two males and two females, settling just 30–40 m north of their original territory and one individual moving 50–60 m east to a territory outside of the plot. However, removing this territory from the analysis did not yield different results ($W=16$, $P=0.088$). Unlike in 2004, after the experiment, the relationship between group size and territory size was no longer significant, even when controlling for treatment type (GLM: whole model: $R^2=0.23$, $F_{3, 10}=1.01$, $P=0.431$).

However, as with experiments conducted during the nonreproductive season (2004), there was a significant treatment effect on the difference in territory size (ANOVA: $R^2=0.45$, $F_{2, 11}=4.12$, $P=0.049$), with territories on plots receiving the heterogeneous treatment decreasing in size, while territories on the even plot increased in size (Fig. 1b). A *post hoc* comparison using Dunnett’s test showed that the spatially heterogeneous plot, but not the even plot, was significantly different from the control at $P=0.05$. Territory expansion occurred principally by individuals incorporating previously unutilized and undefended portions of the plots. The change in food patchiness was again strongly correlated with the average change in territory size during the experiment (GLM: whole model: $R^2=0.42$, $F_{1, 12}=8.09$, $P=0.016$).

Consistent with the results from the nonreproductive season (2004), adult home range overlaps were affected by the experimental treatment (Fig. 2b; ANOVA: $R^2=0.46$, $F_{2, 11}=3.93$, $P=0.053$). A post hoc comparison of treatment means to the control, by Dunnett’s test, indicated that the spatially heterogeneous and even plots were not significantly different from the control at $P=0.05$. The mean adult home range overlap on the heterogeneous treatment plot increased, while mean adult home range overlap on the even plot decreased and they were significantly different from each other (Tukey–Kramers honestly significant difference at $P=0.05$). The change in mean adult home range overlaps within territories was correlated with the changes in territory food patchiness (GLM: whole model: $R^2=0.35$, $F_{1, 12}=5.31$, $P=0.043$).

Discussion

Overall, results of this study indicate that food dispersion exerts a strong effect on the spatial aggregation patterns and

territory size of Gunnison’s prairie dogs. Both male and female adult Gunnison’s prairie dogs showed indistinguishable and significant changes in territory size and spatial overlap in response to experimental changes in food abundance and dispersion and did so whether or not it was the mating season. These experimental results support some key components of the RDH as a potential mechanism for the evolution of group living in this species, while forcing a reassessment of some of the detailed predictions of RDH.

By increasing the average carrying capacity of all territories across experimental plots through increasing food abundance, I could evaluate what effect changes in the distribution of food had on each territory. Unexpectedly, territories on the plots that received patchy and spatiotemporally heterogeneous treatments contracted around the resource patches added, while territories on the plot receiving the even treatment expanded to encompass additional areas where food was being added. While the presence of a significant effect is concordant with the RDH, the outcome was opposite to currently published predictions (summarized in Table 1). The RDH predicts directional changes in territory size based on changes in resource distribution and states that the directions of these changes are contingent on initial patterns of food distribution without providing specific *a priori* expectations (Johnson et al. 2002; see Table 1, predictions 2–4). In general, the results I report here are consistent with the logic of RDH, although the logic is not explained clearly with respect to published predictions. Existing theoretical treatments do not specify what ecological conditions should be associated with particular directional changes in foraging strategies and spatial use. Therefore, this study focused on testing of the predictions for which clear directional hypotheses were provided, as reflected in predictions 2–4 of Table 1. Furthermore, it may be that the response of individuals does not depend on initial conditions but rather on patch size reaching a critical threshold that allows other individuals to utilize the patch. An extension of the RDH model beyond the conventional predictions is required to encompass adaptive foraging responses not currently anticipated.

Theoretical studies have emphasized the tradeoffs associated with territorial defense. As territories become larger, additional defense costs should be incurred, offsetting the potential to gain additional resources (Brown 1964). The expectation is that individuals will be spatially conservative and minimize the area over which they must forage to meet their metabolic needs (Brown 1964; Gill and Wolf 1975; Charnov et al. 1976). However, results of this study suggest that Gunnison’s prairie dogs seek to maximize their energy gain by expanding their ranging and territory size when additional energy makes it beneficial to do so. The ability to

expand territory size without incurring excessive additional defense costs might be associated with vacant marginal space that was not being utilized. On both the control and even plots, such space for expansion was available and territories expanded by individuals incorporating previously unused and undefended areas. Although contrary to the predictions of the RDH, similar responses to changes in resource dispersion have been observed in other species when population sizes were low or below carrying capacity (red fox: Baker et al. 2000; badger: Revilla and Palomares 2002; arctic fox: Eide et al. 2004).

Of particular interest and importance in supporting the RDH as a mechanism to explain group formation was the effect of the treatments on adult home range overlaps. Not surprisingly, because territory size decreased as food patchiness increased, adult home range overlaps correspondingly increased. Therefore, within a territory, it appears that individuals become more spatially tolerant of group members as food becomes increasingly patchy. Within the RDH framework, greater spatial overlap in home ranges, and the resulting closer proximity of individuals to each other, may facilitate a higher frequency of social interactions among individuals, providing the potential for the evolution of increased sociality.

Although resource distribution affected both territory size and home range overlap, the changes in abundance and dispersion did not significantly alter group size. Previous results indicated a strong correlation between territory size and group size that was linked, not to patchiness, but to territory productivity and density (Verdolin 2007). The experiments conducted in this study, emphasizing the effect of resource dispersion, decoupled this relationship by altering territory size in response to the dispersion of food. This decoupling supports the RDH because it is explicitly predicted that territory size will be influenced by the dispersion of resources (Johnson et al. 2001, 2002). A previous experiment that involved mowing the resources on a Gunnison's prairie dog colony did result in a change in group size (Slobodchikoff 1984). In this study, however, I found that group sizes were not strongly affected by increasing abundance or dispersion. The short duration of the experiments may have left little opportunity for population responses to yield significant differences in group size. Given the experimental design, all territories within a given treatment plot were stochastically similar. Because there should have been little incentive for individuals to switch territories, it would have been unlikely to detect significant changes in group size.

For the RDH to apply as a general mechanism, both males and females should respond similarly to changes in resource distribution. If not, RDH might be useful only for one sex, and it might be difficult to distinguish the RDH from other hypotheses that stress male mating strategies as

a determinant of social structure. This assumption is rarely emphasized but is critically important to establishing the RDH as an independent general model for group formation. Results from this study indicate that males and females responded similarly to the experiments across the reproductive and nonreproductive season, suggesting that male mating strategies are not driving spacing patterns. Changes in the demography of groups as a result of the experiments were not related to the original composition of the group. In addition, changes in home range size were not sex specific, indicating that both adult males and females adjusted home ranges in similar ways in response to the food manipulations.

Another key element of the RDH is that there are intrinsic advantages to group living other than benefits more typically assumed for mammalian social groups (e.g., reduced predation risk, access to mates). The RDH is unique in that it requires no additional external force or benefit to explain group living, beyond shared territorial defense in response to patterns of abundance and distribution of resources. Prior to the 2004 experiments, Gunnison's prairie dogs living in larger groups lived on larger territories and had higher per capita food availability. With individuals on larger territories having access to more resources, coupled with no evidence that the per capita rate of intrusions depends on group size, these results provide support in favor of the communal defense assumption of RDH and indicate a potential synergistic benefit associated with living in a larger group.

Unlike in black-tailed prairie dogs, there is little evidence to suggest that Gunnison's prairie dog social groups acquire additional benefits. For example, black-tailed prairie dogs frequently engage in allogrooming with group members (Hoogland 1995). Allogrooming can provide several benefits including the removal of ectoparasites, increased tolerance, strengthening pair bonds, food acquisition, and parental care (Seyfarth and Cheney 1984; Tanaka and Takefushi 1993; De Waal 1997; Henzi and Barrett 1999). Although allogrooming occurs, its incidence in Gunnison's prairie dogs is extremely rare (personal observation) and unlikely to confer any significant benefit.

Infanticide is another seemingly common occurrence among black-tailed prairie dogs (Hoogland 1995) but has not been recorded in Gunnison's prairie dogs despite long-term studies. The lack of infanticide in Gunnison's prairie dogs is not surprising because none of the classical hypotheses for the existence of infanticide appear to apply. Though females could potentially benefit by eliminating the offspring of competing females, because females breed once per year, there is no real chance for males to benefit from infanticide. In addition, females of this species do not appear to regularly nest communally, decreasing the likelihood that infanticide by females would occur.

Increased protection from predators is thought to be a major benefit in many species that live in groups, including black-tailed prairie dogs. Increased vigilance could reduce predation risk for black-tailed prairie dogs living in larger groups within a colony (Hoogland 1979, 1981). For Gunnison's prairie dogs, however, such antipredatory benefits may be largely due to overall colony size and not to group size per se (Verdolin and Slobodchikoff 2002). Thus, reduced predation risk could explain coloniality in these populations, but it does not explain why colonies are subdivided into social groups and communally defended territories.

Lastly, while individuals living in groups clearly have access to potential mates by proximity, behavioral observations (Verdolin 2007), coupled with high levels of extra-group paternity found in previous studies (Haynie et al. 2003; Travis et al. 1995, 1996), indicate that females actively seek copulations with males outside the territory. These data suggest that individuals of either sex may not derive clear benefits of territorial defense via enhanced access to mates. However, a comparison of male mating success (resident males versus nonresident males) will ultimately be the only way to address this issue. Genetic analyses of the reproductive success of individuals from these populations are in progress and perhaps will reveal if access to mates is an additional driving force shaping Gunnison's prairie dog social group formation and maintenance.

If none of the classical benefits for sociality apply, what factors might favor larger group sizes in Gunnison's prairie dogs? They are obligate hibernators, though hibernation is interrupted by cyclic periods of activity (Bakko and Nahorniak 1986). As the season progresses, individuals need to acquire adequate resources to meet their daily requirements and obtain additional resources if they are to survive overwinter hibernation. Therefore, the primary purpose of territories in this species may be to secure sufficient resources and reduce individual defense costs, while constraining the absolute group size possible within a territory by the intensity of competition for those resources. Optimal group size will then be determined by the fitness maximum, based on rates of reproductive output and mortality, that results from access to resources and the costs of group defense as territory size increases (Fig. 3).

Overall, this study provides strong empirical support for the RDH as an explanation of group living in Gunnison's prairie dog. Adult males and females responded to the experiments by adjusting territory size and spatial overlap during both seasons. These changes occurred as both adult males and females modified their home ranges, and there were no consistent differences between adult male and female home ranges, both prior to and during the experiments. Although significant group size changes were not observed, there was no indication that alterations in the composition of groups were sex specific. However, the fact

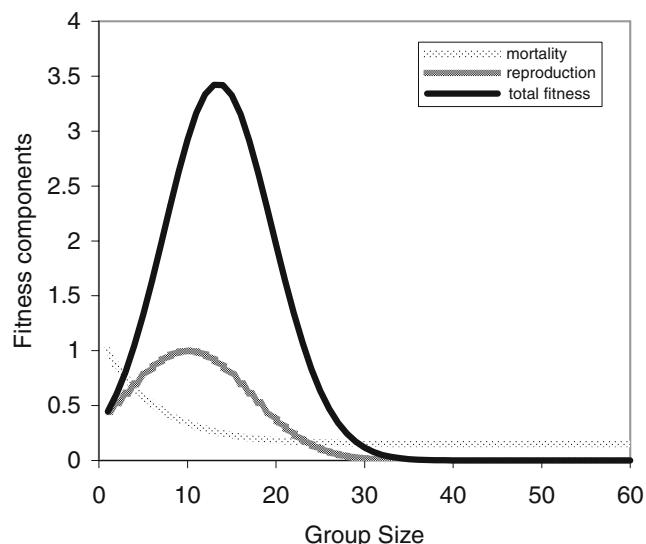


Fig. 3 Conceptual model of selection on group size in an RDH system. It is assumed that in general larger groups inhabit larger territories. Reproduction at first increases with group size because of the benefits of better group defense (lower costs and/or better-quality territories), but eventually competition among group members reduces reproductive success in larger groups. Mortality decreases in larger groups because individuals on larger territories are more likely to find sufficient food regardless of seasonal and annual variations in productivity, although unpredictable climatic events (e.g., floods) place a lower limit on mortality rates. Total fitness (taken simplistically as the reproductive rate divided by mortality, assuming constant vital rates throughout life) peaks at slightly larger group sizes (and presumably territory sizes) than those that maximize reproduction alone

that territories contracted on the patchy and heterogeneous experimental plots suggests that an extension to the current predictions of the RDH is needed to allow for the possibility that, under conditions of superabundant patchy or heterogeneous food availability, individuals will minimize energetic costs and risks associated with territorial defense by reducing territory size. Additionally, because treatments were assigned in such a way as to change initial differences in field conditions toward the most extreme opposite direction, these data provide a foundation for enhancing the RDH model and generating *a priori* expectations about how initial conditions may modify the responses of individuals to changes in resource dispersion and abundance. Lastly, while changes in the abundance of food were similar across treatments, the RDH does not address the potential interaction between simultaneous changes in abundance and dispersion. Future field experiments will be designed to independently assess the impacts of abundance and dispersion as well as potential interactions not currently accounted for in the RDH model.

It has been claimed that the RDH is not a testable hypothesis because it has been used *ad hoc* to explain grouping patterns for which no reasonable alternative

appears to exist. Results of the current investigation suggest that the RDH is a practical, feasible, and testable hypothesis. While it may not be possible to conduct such experimental manipulations for all species, this study demonstrates that the RDH is no longer limited to purely descriptive conclusions and may be applicable to a broader array of species.

Acknowledgements I am grateful to my advisor, Dr. Charles Janson, for his guidance and invaluable contribution to this manuscript. I would also like to thank Drs. Kenneth Armitage, John True, Patricia Wright, and two anonymous reviewers whose comments and suggestions greatly improved this manuscript. For unbelievable field support, veterinary services, and friendship, a heartfelt thank you to Dr. David Washabau. This project could not have been completed without many people dedicating their time and effort, including Bill and Theresa Emig, Carolyn Parker, Perry Crompton, Kristen Hoss, Jessica Hagan, and many others. This study was supported by grants from the American Museum of Natural History, Sigma Xi, and the American Society of Mammalogists. Generous donations of microchips were made by Schlering-Plough and sunflower seeds were kindly provided by Western Organics, Inc. For charitably allowing me use of tomahawk traps, I thank Norris Dodd. Vegetation data were analyzed in the FERTL Lab housed in the Department of Ecology and Evolution, Stony Brook University. Lastly, I thank the City of Flagstaff, Arizona Game and Fish Department and the Arizona State Land Trust Department for all necessary permits. This project was approved by Stony Brook University Animal Care and Use Committee (Permit #1290).

References

- Bacon PJ, Ball F, Blackwell P (1991a) Analysis of a model of group territoriality based on the resource dispersion hypothesis. *J Theo Biol* 148:433–444
- Bacon PJ, Ball F, Blackwell P (1991b) A model for territory and group formation in a heterogeneous habitat. *J Theo Biol* 148:445–468
- Baker PJ, Funk SM, Harris S, White PCL (2000) Flexible spatial organization of urban foxes, *Vulpes vulpes*, before and during an outbreak of sarcoptic mange. *Anim Behav* 59:127–146
- Bakko EB, Nahorniak J (1986) Torpor patterns in captive white-tailed prairie dogs (*Cynomys leucurus*). *J Mamm* 67:576–578
- Bradbury JW, Vehrenamp SL (1976) Social organization and foraging in emballonurid bats II. A model for the determination of group size. *Behav Ecol Socio* 2:383–404
- Brown JL (1964) The evolution of diversity in avian territorial systems. *Wilson Bull* 76:160–169
- Brown JL (1982) Optimal group-size in territorial animals. *J Theo Biol* 95:793–810
- Carr GM, Macdonald DW (1986) The sociality of solitary foragers—a model based on resource dispersion. *Anim Behav* 34:1540–1549
- Charnov EL, Orians GH, Hyatt K (1976) Ecological implications of resource depression. *Am Nat* 110:247–259
- Crook JH (1965) The adaptive significance of avian social organizations. *Symp Zool Soc London* 14:181–281
- da Silva J, Woodroffe R, Macdonald DW (1993) Habitat, food availability and group territoriality in the European badger, *Meles meles*. *Oecologia* 95:558–564
- Davies NB, Hartley IR (1996) Food patchiness, territory overlap and social systems: an experiment with dunnocks *Prunella modularis*. *J Anim Ecol* 65:837–846
- de Waal FB (1997) The chimpanzee's service economy: food for grooming. *Evol Human Behav* 18:375–386
- Eide NE, Jepsen JU, Prestrud P (2004) Spatial organization of reproductive Arctic foxes *Alopex lagopus*: responses to changes in spatial and temporal availability of prey. *J Anim Ecol* 73:1056–1068
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and evolution of mating systems. *Science* 197:215–223
- Gill FB, Wolf LL (1975) Foraging strategies and energetics of East-African sunbirds at mistletoe flowers. *Am Nat* 109:491–510
- Haynie ML, Van den Bussche RA, Hoogland JL, Gilbert DA (2003) Parentage, multiple paternity, and breeding success in Gunnison's and Utah prairie dogs. *J Mamm* 84:1244–1253
- Henzi SP, Barrett L (1999) The value of grooming to female primates. *Primates* 40:47–59
- Hoogland JL (1979) The effect of colony size on individual alertness of prairie dogs (Sciuridae: *Cynomys* spp.). *Anim Behav* 27:394–407
- Hoogland JL (1981) The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology* 62:252–272
- Hoogland JL (1995) The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago, p 557
- Hoogland JL (1999) Philopatry, dispersal, and social organization of Gunnison's prairie dogs. *J Mamm* 80:243–251
- Janson CH (1992) Evolutionary ecology of primate social structure. In: Smith EA, Winterhalder B (eds) Evolutionary ecology and human behavior. Aldine de Gruyter, New York, pp 95–130
- Johnson DDP, Macdonald DW, Newman C, Morecroft MD (2001) Group size versus territory size in group-living badgers: a large-sample field test of the resource dispersion hypothesis. *Oikos* 95:265–274
- Johnson DDP, Kays R, Blackwell PG, Macdonald DW (2002) Does the resource dispersion hypothesis explain group living? *TREE* 17:63–570
- Krebs CJ (1999) Ecological methodology. Addison-Wesley Educational, Reading
- Kruuk H, Parish T (1982) Factors affecting population density, group size and territory size of the European badger, *Meles meles*. *J Zool* 196:31–39
- Kruuk H, Parish T (1987) Changes in the size of groups and ranges of the European badger, *Meles meles*, in an area in Scotland. *J Anim Ecol* 56:351–364
- Lott DF (1991) Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press, Cambridge
- Macdonald DW (1983) The ecology of carnivore social behavior. *Nature* 301:379–384
- Macdonald DW (1984) Carnivore social behavior—does it need patches—reply. *Nature* 307:390–390
- Maher CR, Lott DF (2000) A review of ecological determinants of territoriality within vertebrate species. *Am Midl Nat* 143:1–29
- Myers JP, Connors PG, Pitelka FA (1981) Optimal territory size in the sandpiper: compromises in a variable environment. In: Kamil AC, Sargent D (eds) Foraging behavior. Garland STPM, New York, pp 135–158
- Nagy KA, Girard IA, Brown TK (1999) Energetics of free-ranging mammals, reptiles, and birds. *Ann Rev Nutr* 19:247–273
- Owens D, Owens M (1996) Social dominance and reproductive patterns in brown hyenas, *Hyena brunnea*, of the central Kalahari desert. *Anim Behav* 51:535–551
- Packer C, Scheel D, Pusey AE (1990) Why lions form groups—food is not enough. *Am Nat* 136:1–19
- Rayor LS (1988) Social organization and space-use in Gunnison's prairie dog. *Behav Ecol Socio* 22:69–78
- Revilla E, Palomares F (2002) Spatial organization, group living and ecological correlates in low-density populations of Eurasian badgers, *Meles meles*. *J Anim Ecol* 71:497–512

- Sánchez-Prieto CB, Carranza J, Pulido FJ (2004) Reproductive behavior in female Iberian red deer: effects of aggregation and dispersion of food. *J Mamm* 85:761–767
- Seaman DE, Powell RA (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085
- Seaman DE, Millspaugh JJ, Kernohan BJ, Brundidge GC, Raedke KJ, Gitzen RA (1999) Effects of sample size on kernel home range estimators. *J Wildl Manag* 63:739–747
- Seyfarth RM, Cheney DL (1984) Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature* 308:541–542
- Slobodchikoff CN (1984) Resources and the evolution of social behavior. In: Price PW, Slobodchikoff CN, Gaud WS (eds) *A new ecology: novel approaches to interactive systems*. Wiley, New York, pp 227–251
- Stouffer PC, Romagnano LC, Lombardo MP, Hoffenberg AS, Power HW (1988) A case of communal nesting in the European starling. *Condor* 90:241–245
- Tanaka I, Takefushi H (1993) Elimination of external parasites (lice) is the primary function of grooming in free-ranging Japanese macaques. *Anthro Sci* 101:187–193
- Tileston JV, Lechleitner RR (1966) Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado. *Am Midl Nat* 75:292–316
- Travis SE, Slobodchikoff CN (1993) Effects of food resource distribution on the social system of Gunnison's prairie dog (*Cynomys gunnisoni*). *Can J Zool* 71:1186–1192
- Travis SE, Slobodchikoff CN, Keim P (1995) Ecological and demographic effects on intraspecific variation in the social system of prairie dogs. *Ecology* 76:1794–1803
- Travis SE, Slobodchikoff CN, Keim P (1996) Social assemblages and mating relationships in prairie dogs: a DNA fingerprint analysis. *Behav Ecol* 7:95–100
- van Schaik CP, Janson CH (2000) Infanticide by males and its implications. Cambridge University Press, Cambridge
- Verdolin JL (2007) Resources, not male mating strategies, are a determinant of social structure in Gunnison's prairie dogs (*Cynomys gunnisoni*). *Behav* 144:1361–1382
- Verdolin JL, Slobodchikoff CN (2002) Vigilance and predation risk in Gunnison's prairie dogs (*Cynomys gunnisoni*). *Can J Zool* 80:1197–1203
- Verdolin JL, Slobodchikoff CN (2009) Resources, not kinship, determine social patterning in the territorial Gunnison's prairie dog (*Cynomys gunnisoni*). *Ethology* 115:59–69
- Von Shantz T (1984) Carnivore social behaviour—does it need patches? *Nature* 307:389–390
- Waser PM (1977) Feeding, ranging, and group size in the mangabey *Cercocebus albigena*. In: Clutton-Brock TH (ed) *Primate ecology*. Academic, New York, pp 183–222
- Waser PM (1988) Resources, philopatry and social interactions among mammals. In: Slobodchikoff CN (ed) *Ecology of social behavior*. Academic, New York
- Woodroffe R, Macdonald DW (2000) Helpers provide no detectable benefits in the European badger (*Meles meles*). *J Zool* 250:113–119
- Worton B (1995) Using Monte Carlo simulations to evaluate kernel-based home range estimators. *J Wildl Manag* 59:794–800
- Yamagiwa J, Hill D (1998) Intraspecific variation in the social organization of Japanese macaques: past and present scope of field studies in natural habitats. *Primates* 39:257–273