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EFFECTS OF PREDATION RISK AND GROUP SIZE ON THE FORAGING BEHAVIOUR OF BLACK-TAILED PRAIRIE DOGS (Cynomys ludovicianus)

by

STEWART DEAN KILDAW

A thesis submitted to the Faculty of Graduate Studies and
Research in partial fulfilment of the requirements for
the degree of Master of Science.

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Effects of predation risk and group size on the foraging behaviour of black-tailed prairie dogs" submitted by S. Dean Kildaw in partial fulfilment if the requirements for the degree of Master of Science.

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ABSTRACT

I investigated the relationship between the foraging behaviour of black-tailed prairie dogs and several factors that likely influence risk of predation. Using a correlative approach, I examined the relationship between a forager's level of alertness and a number of observation-specific contextual variables. Alertness was correlated poorly with all measured variables ($r^2 < 0.15$); however, when correlation coefficients from 6 different groups were pooled, trends in their distribution suggested that prairie dogs foraged more alertly when wind velocity was greater, when temperature was cooler, when they were nearer to the edge of the colony, when they were further from burrows, and when there were few individuals within 40m. Of nine measures of group size that varied with respect to the distance and age class of enumerated individuals, alertness was most strongly related to the number of adults within 20m of the focal individual. This relationship weakened with increasing distance and was non-existent for measures of group size that enumerated pups only. Overall, my results indicate that foraging prairie dogs may be responsive to the measured factors, but any conclusions must await experimental analyses or a correlative study that incorporates forage abundance and quality as well as risk of predation.

I experimentally manipulated group size and found that prairie dogs foraged more conservatively (more alertly and in less risky places) when in small vs large groups. The response of prairie dogs to reductions of group size was reversible and, following permanent reductions of group size, persisted for at least three weeks. I conclude that a causal relationship exists between group size and foraging behaviour such that individuals in large groups forage less conservatively than those in smaller groups. Because less conservative foragers are likely more efficient foragers, I suggest that enhanced foraging efficiency is an advantage of group living in black-tailed prairie dogs.

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TABLE OF CONTENTS

LIST OF TABLES

Appendix B:

(list of tables cont.)

Appendix C:

LIST OF FIGURES

(list of figures cont.)

Appendix A:

I. GENERAL INTRODUCTION

Black-tailed prairie dogs (Cynomys ludovicianus, "prairie dogs" hereafter) are large (ca. 700-1000 grams), semi-fossorial herbivores that are diurnal and densely colonial. Prairie dogs are at risk to predators when foraging because they must leave the safety of burrows to acquire food. Away from burrows they are easy prey if surprised by a predator because they are not cryptic, are slow runners, and lack chemical or physical defenses. Prairie dogs avoid predators by detecting them at a distance and escaping to the safety of nearby burrows (King 1955).

Foraging prairie dogs periodically assume "alert" postures from which they have a greater range of visibility because their eyes are elevated above the surrounding vegetation. Commonly, prairie dogs are assumed to be looking for predators when alert (Hoogland 1979, 1981); however, individuals might engage in alertness for a number of other reasons (Underwood 1982). In any case, individuals who are more alert when foraging are likely better able to detect predators and hence would be less at risk.

Foraging prairie dogs must not only avoid predators, they must also obtain sufficient quantities of food. Because alert postures reduce the amount of time available for feeding, highly alert individuals are likely less efficient foragers (Bertram 1980, Lima and Dill 1990). Thus, as is the case for many species that are at risk to predators when foraging, prairie dogs are faced with a tradeoff between safety and efficiency (Sih 1980, Holmes 1984, Lima and Dill 1990). A compromise between these two components of fitness would be adaptive because neglecting either would, for obvious reasons, be deleterious.

Natural selection would favour individuals who balance safety and foraging efficiency such that they obtain the greatest amount of energy and expose themselves to the least risk of predation. To maximize fitness, foraging prairie dogs should compromise these two fitness goals in a manner that reflects the ratio of investment to return for each: for a given risk of predation and a given energetic demand there should exist a particular mix of foraging and alertness that is optimal.

Many factors that have the potential to influence the investment/ return ratio of both risk and energy intake vary seasonally, daily, or minute-by-minute. It would be adaptive for prairie dogs to alter their behaviour such that they forage optimally despite short term fluctuations in risk and foraging factors. Indeed, the level of alertness exhibited by foraging individuals is highly variable and is believed to be influenced by both risk and energetic demand for ground squirrels (Hoogland 1979, Holmes 1984, Carey and Moore 1986) and other species (Grubb and Greenwald 1982, Lima 1988a,b).

In this thesis I examine the relationship between factors that may influence risk of predation and, hence, the foraging behaviour of black-tailed prairie dogs. In the second chapter I present a correlative analysis of the relationship between several risk factors and the level of individual alertness of foraging prairie dogs. The foraging behaviour of free ranging prairie dogs was quantified and correlated with measures of group size and several other factors that could influence risk.

The third chapter describes an experimental study of the relationship between group size and the foraging behaviour of prairie dogs. Both theory (Pulliam 1973) and empirical evidence (Hoogland 1981) suggests that individuals in large groups are less at risk to predators and might adopt different foraging behaviours as a consequence. Prairie dogs can behaviourally compensate for manipulation-induced changes in risk by altering individual alertness, the height of vegetation they forage in, their distance from an escape burrow, and their distance to the edge of the colony. Because these behaviours are possible determinants of foraging efficiency as well as risk, the interpretation of behavioral responses to group-size manipulations can be extrapolated to the more general questions, "is enhanced foraging efficiency an advantage of group living?" and "why do prairie dogs live in groups?"

Furthermore, because I have addressed the relationship between alertness and group size with both a correlative and an experimental approach, the strengths and weaknesses of each can be compared directly.

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II. CONTEXTUAL CORRELATES OF THE FORAGING BEHAVIOUR OF BLACK-TAILED PRAIRIE DOGS (Rodentia: Cynomys ludovicianus)

INTRODUCTION

Black-tailed prairie dogs (Rodentia: Cynomys ludovicianus, "prairie dogs" hereafter) are diurnal, semi-fossorial herbivores that are densely colonial and are at risk to predators when foraging. They are defenceless if surprised at close range by a predator and avoid being preyed upon by visually detecting approaching or concealed predators at a distance and escaping to the safety of nearby burrows (King 1955).

For prairie dogs, as with many species that are simultaneously a predator and potential prey when foraging, the goals of avoiding predators and foraging efficiently conflict. Individuals that reduce their risk of predation by foraging more alertly would likely forage less efficiently because they would have less time to devote to feeding (Powell 1974, McNamara and Houston 1986). Similarly, prairie dogs that reduce their risk to predators by foraging near to refuge would likely forage less efficiently because preferential foraging in the vicinity of burrows has likely diminished the quantity and quality of available forage (Andrusiak and Harestad 1989, Devenport 1989). Foraging prairie dogs are faced with a fitness tradeoff - they may be unable to maximise both safety and foraging efficiency because foraging strategies that enhance one of these fitness components are adopted at the expense of the other. A compromise between the two would be optimal because neglecting either would likely diminish reproductive success or place the forager's life in jeopardy (Sih 1980).

Natural selection should act to optimize foraging behaviour in the face of fluctuations in the risk of predation that occur on an ecological time scale. Natural selection might also act to relieve the severity of the tradeoff by selecting for adaptations that reduce risk. Indeed, predation has long been considered an important selective force and has been implicated in the evolution of many diverse and conspicuous morphological, physiological, life history, and behavioral characteristics (Edmunds 1974). That prairie dogs construct underground burrows, live in groups, have keen eyesight, and periodically interrupt foraging to become alert have all been interpreted as adaptations to avoid predators (King 1955, Hoogland 1981).

A number of factors that influence the level of risk experienced by a foraging prairie dog fluctuate on a fine time scale. For example, group size and the position of a forager within the group are potential risk determinants (Lima and Dill 1990) that can change rapidly. Factors that influence a forager's ability to detect predators may also fluctuate on a short time scale - wind speed (King 1955), light intensity (Lima 1988b), the height of surrounding vegetation (Metcalfe 1984, Carey and Moore 1986), the forager's level of alertness (Fitzgibbon 1989), and the forager's proximity to areas that might conceal predators (Lima and Dill 1990) are examples. Other variable risk factors include the forager's running ability, its proximity to refuge, and factors that reflect the likelihood or imminence of an predatory attack - the abundance and diversity of predators in the area, the alert behaviour and alarm calls of nearby foragers (Loughry and McDonough 1988), and the forager's awareness of a nearby predator for instance.

Clearly, it would be adaptive for prairie dogs to have the capacity to alter their foraging behaviour in a manner that compensates for seasonal, daily and hourly fluctuations in factors that influence risk. In order to optimise foraging behaviour in the face of fluctuating risk factors, prairie dogs must assess their immediate risk to predators and incorporate risk into their behavioral decision-making.

Lima and Dill (1990) recently reviewed a wealth of evidence that suggests that animals are sensitive to risk of predation when making behavioral decisions. Many of these studies investigated how, in the context of a safety-foraging efficiency tradeoff, an individual's immediate risk of predation influences its foraging behaviour.

Prairie dogs can behaviourally alter their risk of predation in two ways: a) they can determine **where** they forage - how near they are to safety, visual obstructions, and cover that potentially conceals predators - and b) they can vary their level of alertness when foraging. Individual alertness is one of the most direct and well studied ways that foraging prairie dogs can manipulate their immediate risk of predation (Lima and Dill 1990).

In this study I investigated the relationship between individual alertness and several factors that potentially influence a foraging prairie dog's risk of being preyed upon. My approach was correlative. I measured individual alertness and the following likely risk factors: a) wind speed - prairie dogs may be more at risk to predators on windy days because their capacity to hear alarm vocalizations or detect the movements of stalking predators might be compromised (King 1955);
b) temperature - because of a suspected positive correlation between temperature and light intensity, prairie dogs might be more at risk during cool (low light intensity) periods because their ability to detect predators might be compromised (Lima 1988b) (temperature replaced light intensity as a factor, post facto, because light intensity data was not available for many observations); c) the prevalence of alarm calling - alarm calls indicate that a predator is in the vicinity, and hence, a heightened risk of predation; d) the forager's proximity to the edge of the colony - prairie dogs may be more at risk to predators when near the colony edge where they are nearer to concealment cover for predators (Holmes 1984) and benefit less from being in a group (Hoogland 1979, Fitzgibbon 1989); e) the forager's proximity to a burrow - risk likely decreases with decreasing distance to a burrow because the time it takes to reach safety is reduced; f) vegetation height - risk is likely greater in taller vegetation because a prairie dog's ability to detect predators or alarm signals of conspecifics is compromised (Underwood 1982, Carey and Moore 1986); and g) number of neighbours - foragers with many neighbours may be less at risk to predators by a number of mechanisms (Bertram 1978, Hoogland 1979).

If foraging prairie dogs respond behaviourally to increasing risk of predation I predict the amount of time devoted to alertness will be negatively correlated with (and feeding will be positively correlated with) distance from the edge of the colony, temperature, and group size. Furthermore, I predict that alertness will be positively correlated with (and feeding will be negatively correlated with) wind speed, alarm calling, distance from refuge, and vegetation height.

MATERIALS AND METHODS

The Study Area

During the summers of 1989 and 1990 prairie dogs were studied at Wind Cave National Park in southwestern South Dakota (43° 35' N latitude, 103° 25' E longitude, elev. 1100 - 1500m). The park lies on the southeastern edge of the Black Hills and straddles the ecotone of ponderosa pine forest (Pinus ponderosa) and northern mixed grass prairie. The park is home to bison (Bison bison), elk (Cervus elaphus), pronghorn (Antilocapra americana), and a number of terrestrial and aerial prairie dog predators. See King (1955) for a more complete description of the area.

Although prairie dogs are protected within the park, they are managed as a pest species and the size of their colonies is controlled by poisoning and shooting. Colonies used in this study had not been managed for at least four years.

Groups

Behavioral data was collected from six groups of prairie dogs. Groups were defined by the isolation of their members from other prairie dogs. Two groups were >2 km from other prairie dogs while the remaining 4 groups were peripheral fragments of much larger colonies. Although individuals in peripheral groups were visually isolated from nearby prairie dogs, they were within hearing range of hundreds of extra-group animals. Groups contained 10 - 48 adults (mean = 23.6, yearlings included), 16 - 76 pups (mean = 32.3), and covered an area of 0.89 - 1.5 ha (mean = 1.1 ha).

Trapping and Marking

Prairie dogs were captured in Tomahawk live traps (models 102, 103 and 104) baited with whole oats. Traps were distributed uniformly throughout a group's active area at a density of 100/ha. Most were set within 1 - 2m of well-used burrow entrances and initially were wired open and filled with oats during a 3 - 5 day habituation period prior to active trapping.

The mass of captured prairie dogs was measured to the nearest 10 grams with a Pesola 1500g spring scale, their sex was recorded, and the width of their heads (across the zygomatic arches) was measured with plastic vernier callipers. Prairie dogs had numbered metal tags placed in both ears (National Band and Tag Co. style 1005-1) and were given an individually distinctive dye mark (Nyanzol A) on their fur.

Grids and blinds

An observation blind and a grid of colour-coded, 24"-tall wooden stakes spaced 20m from one another were established at each group. For five groups, low plywood walls (24" tall and 17' long) served as blinds. At one group with no nearby vantage point, an observation seat was placed three metres off the ground in a nearby ponderosa pine (Pinus ponderosa). When seated at any blind, only the top half of an observer's head was visible to the prairie dogs. A t-shirt "scarecrow" was left flapping in the wind behind each blind to habituate prairie dogs to the silhouette and movements associated with the presence of an observer.

Preliminary Observations

Prairie dogs were further habituated to the presence of an observer during 3 - 5, three-hour-long preliminary observation sessions. Observers monitored the interactions and movements of prairie dogs to determine the location of coterie boundaries and the coterie affiliation of individuals. For the purpose of behavioral observations, one coterie in each group was designated the "focal coterie" on the basis of the following criteria (ordered from most to least important): preferred coteries were (a) entirely visible from the blind, (b) farthest from or better isolated from extra-group individuals, (c) located nearest to the centre of the group, and (d) contained between 4 and 6 adults. Focal coteries each contained between 5 and 9 adults (mean = 5.8), between 7 and 11 pups (mean = 8.7), were between 0.20 and 0.46 ha (mean = 0.28 ha) in area, and had a burrow entrance density of between 133 and 232/ha (mean = 181/ha).

Behavioral Observations

Behavioral data were collected during three-hour-long morning (7am - 11am) and evening (4pm - 8pm) observation sessions. During the summer months prairie dogs were most active at those times, spending more time in their cool burrows during the heat of the day (King 1955).

Foraging behaviour was quantified using "focal animal sampling" (Altmann 1974). The foraging behaviour of a selected individual was monitored for a pre-determined period of time during which the time of initiation and termination of all bouts of behaviour were recorded. Focal observations collected from groups 1-4 during July and August of 1989 were each five minutes long while those collected from groups 5 and 6 during June of 1990 were each three minutes long. After my first field season, I discovered that an observation duration of 3 minutes was optimal (Appendix A). Fifteen (1989) or twenty (1990) focal observations could be gathered during each three-hour-long watch session.

During each watch session an attempt was made to balance the number of observations collected on different focal animals. The individual who had been observed the fewest number of times during a particular session was preferentially selected as the subject of the next focal observation; however, data were collected from lower priority individuals if the highest priority individual was out of sight or not actively foraging when an observation was about to be initiated.

A focal observation was initiated only when a group was calm and the selected focal animal was actively foraging. It was interrupted in the event of a disturbance or if the focal animal otherwise suspended foraging activities - periodically, foraging prairie dogs would run to or down burrows, engage in prolonged social interactions, and become alert for more than 10 seconds in an investigative manner. Interrupted observations were resumed if the group and focal animal returned to feeding within five minutes of the disturbance. If not, the observation was terminated at that point and another was initiated when the group had settled. I discarded truncated observations that were less than 2/3 complete.

Prairie dogs were observed with the aid of tripod-mounted 10 x 50 wide angle binoculars. Foraging postures, non-foraging behaviours, and vocalizations were monitored and keyed directly into a Tandy 102 lap top computer as they occurred. An event recording program associated particular activities and occurrences with keys on the computer and produced a summary of each focal observation.

The following behaviours were monitored during focal observations:

a) foraging postures;

Feeding - spine parallel to the ground with head depressed more than 45° from horizontal.

Headbob - spine parallel to ground with head depressed less than 45° from horizontal **while chewing** or processing food.

Upright - standing/resting on haunches with both fore-legs off the ground **while chewing** or handling food. Spine usually inclined more than 45° from horizontal.

Alert - Headbob and Upright postures that do not involve chewing or processing food.

b) non-foraging behaviours;

Amicable - greeting, allo-grooming.

Agonistic - territorial disputes, tooth rattling, chasing.

Moving - walking with head up or loping for short distances.

Other - a catch all category including grooming, on mound, stretching, chasing insects.

c) vocalizations;

Jump-yip - the focal animal tilts its head back, throws its front legs and upper body skyward, and emits a nasal, two-syllable, bark-like vocalization.

Jump-yip by Others - a "jump-yip" given by individuals in or near the group.

Alarm Call - a single alarm bark given by an individual in or near the group.

Repetitive Alarm Call - A rhythmic series of alarm calls that often persists for several minutes. Given by individuals in or near the group.

Extrinsic Factors

Measurements of 15 risk-influencing factors were appended to each observation upon its completion. I noted the distance from the focal animal to the edge of the colony (Distcol), whether it had foraged within 1.5 m of a burrow for most of the observation or not (Distbur), and the height of vegetation that it had foraged in (Veghigh)(vegetation above eyes when in Feeding (Veghigh=1) and Headbob (Veghigh=2) postures). I recorded the number of other prairie dogs (pups and adults were enumerated separately) that were within 20m of the focal animal (Near Adults, Near Pups, Total Near), that were within 40m of the focal animal (Distant Adults, Distant Pups, Total Distant), and that were present in the entire group (Colony Adults, Colony Pups, Total Colony). Measurements of wind speed (Wind) and temperature (Temp) were recorded hourly during every observation session and, via linear interpolation, were appended to each focal observation at a later time. Lastly, the proportion of time that alarm calls of any kind occurred (Calls) was calculated.

Treatment of the Data

Behavioral data were modified prior to statistical treatment. The frequency of all recorded **events** was converted to the number of occurrences per minute of observation. Three summary statistics (measures of behaviour) were calculated for all recorded **behaviours**:

a) The number of bouts of the behaviour that occurred during each minute of observation, b) the average length of bouts of the behaviour, and c) the percentage of the total length of an observation that was devoted to the behaviour (note: the percentage of time devoted to Feeding, Headbob, Upright, and Alert behaviours was calculated as a portion of the total time devoted to these four behaviours, not the total length of the observation). The following 6 measures of behaviour were treated in statistical analyses: 1) Percentage of foraging time devoted to Feeding (% Feeding); 2) Bouts of Feeding per minute of observation (#/min Feeding); 3) Average duration of bouts of Feeding (Ave. Feeding); 4) Percentage of foraging time devoted to Headbob (% Headbob); 5) Percentage of foraging time devoted to Upright (% Upright); and 6) Percentage of foraging time devoted to Alert (% Alert);

Statistical Analysis

To determine whether behaviours and factors were linearly related, for each group correlation coefficients (r) were computed between each of the 6 measures of behaviour and each of the 15 measured factors. Because Veghigh and Distbur were categoric variables, I compared measures of behaviour between the two states of each of these factors with two-group T-tests.

To determine whether a nonlinear relationship between a behavior and a factor may have confounded my linear correlation analysis, I partitioned the range of each factor into several classes such that the largest and smallest class contained at least 10 observations and intermediate classes spanned equal intervals. Observations were then pooled by class and means for each measure of behaviour were calculated, and graphed. For regions of a graph for which there appeared to be a relationship between the behavior and the factor, I discarded all other observations and recalculated correlation coefficients.

To investigate whether interactions between factors obscured their individual relationships with measures of behaviour, I computed partial correlation coefficients between each factor and each measure of behaviour, partialling out all other factors.

RESULTS

The foraging behaviour of prairie dogs was highly variable throughout the range of all measured environmental factors. For all six groups, there were no strong correlations between the six measures of foraging behaviour and the fifteen potential risk-influencing factors (Table 2.1). Although a number of correlation coefficients (r) were statistically significant (owing to large sample sizes), none were greater than 0.35. The largest r^2 value - roughly the proportion of variation in one variable that can be explained by variation in a second variable - was less than 0.13. The r^2 values computed for most behaviour-factor relationships were less than 0.01.

Patterns exist in the data when, for a given factor, the correlation coefficients for all 6 measures of behaviour and for all 6 groups are considered as a whole. By chance alone one would expect at least two of the 36 correlation coefficients computed for each factor to be statistically significant. That every factor has at least three associated significant coefficients (Table 2.1), and that 6 factors had 10 or more associated significant correlation coefficients suggests that certain factors were non-randomly associated with foraging behaviours.

Within the correlation table of each factor I looked for consistency among coefficients that would suggest a relationship between that factor and foraging behaviour. If a factor were positively correlated with alertness, I predicted that as the factor increases prairie dogs should reduce the percentage of foraging time they devote to Feeding and should increase the percentage of time they devote to Headbob, Upright, and Alert. Furthermore, because active foraging is interrupted by a greater number of bouts of alertness, bouts of Feeding should become more numerous and shorter in duration. If a factor were negatively related with alertness, I predicted that the correlations between the factor and the 6 measures of behaviour would be opposite to those outlined above.

For each factor I determined the total number of correlation test statistics that were greater than or equal to 0.10 (and for Distbur and Veghigh, the number of T-test statistics that were greater than 1.5) and, of these, determined the number that were positively or negatively associated with alertness (these criteria were subjectively determined). One would expect that if there were no relationship between a factor and foraging behaviour then correlation coefficients would be symmetrically distributed about a mean of 0 (there would be an equal number of positive and negative coefficients). A heavily skewed distribution of correlation coefficients would suggest that the factor and the behaviour were related.

The asymmetric distribution of correlation coefficients for several factors suggests that factors varied predictably with the foraging behaviour of prairie dogs. The degree of skewness of the distribution of correlation coefficients was measured with a binomial test. Distributions for which the binomial test was significant were considered to be "highly skewed", indicating a possible correlation between the factor and the behaviour.

Wind

Nine of 13 Wind correlation coefficients that were greater or equal to 0.10 were positively correlated with alertness. The distribution of these coefficients is highly skewed ($p=0.05$), suggesting a positive association between wind and alertness (Table 2.1).

Temperature

Fifteen of 17 Temp coefficients that were greater than or equal to 0.10 indicated it was negatively associated (highly skewed, $p=0.001$) with alertness (Table 2.1). Although this result agrees with my prediction, the premise on which the prediction was based, that Temp and light intensity were positively correlated, proved to be invalid. The correlation between Temp and light intensity was strong and positive ($r > 0.30$) for 4 groups but strong and negative ($r > 0.30$) for two others. On the other hand, the relationship between Temp and alertness was positive for all 6 groups (Table 2.1). Taken together these data suggest that light intensity does not underlie the relationship.

Calls

Of 6 coefficients that were 0.10 or greater, 5 were positively correlated with alertness (Table 2.1). Despite the strong directional trend in these data, they do not argue strongly that Calls and alertness are associated because too few coefficients satisfied the r = 0.10 inclusion criterion to make a judgement.

Distance from Colony Edge and Distance from Burrow

In agreement with my predictions Distcol was negatively and Distbur positively related to alertness. Of 20 Distcol coefficients that were greater than or equal to 0.10, 16 (p=0.005) were negative with respect to alertness (Table 2.1). Of 9 Distbur T-test statistics that were greater than 1.5, 8 (p=0.02) indicated a positive relationship with alertness.

Vegetation Height

Seven of 17 T-test statistics that were greater than 1.5 (p=0.15) were negatively associated with alertness. These data do not suggest that there is a relationship between Veghigh and feeding because the distribution of T-test values was not highly skewed.

Group Size

Correlation coefficients were computed between foraging behaviour and 9 measures of group size that differed from one another with respect to the distance from the focal animal that neighbouring individuals were considered part of its "group", and with respect to whether only adults, only pups, or all individuals were enumerated.

Adults

Of all group size measures, Near Adults (the number of adults within 20m of the focal animal) was the most strongly correlated with foraging behaviour. All 16 correlation coefficients that were 0.10 or greater indicated a negative relationship between Near Adults and alertness (p=0.0005) (Table 2.2). The strength of this relationship was weaker for measures of group size that included individuals more distant from the focal animal. For Distant Adults (the number of adults within 40m of the focal animal) only 12 of 18 (p=0.07) coefficients that were 0.10 or greater indicated a negative relationship between this factor and alertness. When the number of adults present on the entire colony was used as the measure of group size, only 10 correlation coefficients were greater than or equal to 0.10. Of these only six suggested that there was a negative relationship between alertness and this measure of group size (Table 2.2).

Pups

In contrast to adult group size measures, those enumerating pups did not vary predictably with prairie dog foraging behaviour. For all three distance classes few correlation coefficients were 0.10 or greater, and of those the ratio of those positive to those negative was near equality (Table 2.2).

Total Group Size

Not surprisingly, group size measures that enumerated both adults and pups generated data intermediate to those that included only adults or pups (Table 2.2). Given the differing effects of pups and adults on foraging behaviour, the results for measures of total group size are not readily interpretable.

Truncation Analyses

Truncation analyses were not fruitful because variation among observations that was to an extent masked by large sample sizes, became more of a factor when sample size was reduced. Truncated data produced few correlation coefficients that were 0.10 or greater and acted to cloud, not clarify, relationship between factors and measures of behaviour.

Partial Correlation Analyses

No partial correlations coefficients were larger than 0.35, suggesting that interactions between measured factors did not weaken the relationships between behaviours and factors. Further multivariate analyses seem unlikely to explain a substantial amount (>50%) of the variation in foraging behaviour present among observations.

DISCUSSION

Trends in the distribution of correlation coefficients suggest that several factors affected the level of alertness of foraging prairie dogs. Furthermore, because the polarity of these correlations indicates that prairie dogs forage more alertly as risk increases, my results suggest that prairie dogs are sensitive to the risk of predation when making foraging decisions.

However, because the analyses are correlative and lack statistical rigour, the interpretations to follow are not conclusive; rather these exploratory analyses are useful primarily for forming hypotheses for future testing.

Wind

Prairie dogs tended to increase their level of alertness as wind speed increased, suggesting that individuals may be sensitive to this factor when making foraging decisions. Prairie dogs are likely more at risk to predators on windy days because their ability to hear distant alarm calls or detect predators, whose motions may be less apparent when in a sea of waving grass, may be compromised (King 1955). I conclude that the positive correlation between Wind and alertness is best interpreted as a compensatory response of foraging prairie dogs to increasing predation risk.

Temperature

A priori, I predicted that Temp, because of an expected correlation with light intensity, would be negatively associated with alertness. Prairie dogs might be less able to detect distant predators when light intensity is low and as a consequence might forage more alertly. (Lima 1988a,b)

However, Temp and light intensity proved to be poorly correlated. Separating observations into morning and evening periods and re-analyzing the data, improved the correlation between Temp and light intensity, but not enough to explain the relationship between Temp and alertness. An alternate interpretation is required to explain these data.

Temp may be associated with alertness by a mechanism that has nothing to do with light intensity or an individual's ability to detect predators. During the heat of the day the above-ground activity of prairie dogs is constrained by their need to thermoregulate (Belovsky, unpublished ms.); they avoid overheating by periodically cooling off in burrows (King 1955). Time spent in burrows reduces the total amount of time available for foraging. A negative relationship between alertness and temperature may arise because prairie dogs compensate for lost foraging time by reducing their level of alertness when above ground feeding, thereby enhancing their rate of food intake. This interpretation is corroborated by the fact that for all six groups Temp was negatively correlated with measures of group size (Near adults and Total colony in particular). Group size should be smaller when temperature is greater because at any one time a greater proportion of individuals are cooling off in burrows. Apparently, the effect of Temp on foraging behaviour is greater than and in an opposite direction to that of group size; however further study is required to determine the nature of this relationship.

Calls

The foraging behaviour of prairie dogs was not related to Calls. On the other hand, California ground squirrels forage more alertly during bouts of alarm calling (Loughry and McDonough 1988). That my data did not indicate a similar trend is likely a consequence of fact that I took pains to not collect data from prairie dogs that were conspicuously paying heed to repetitive alarm calls. Furthermore, observations were interrupted when foragers were distracted by incipient alarm calls. Prairie dogs will pay attention to recently initiated alarm calls but soon ignore the call if danger is not apparent (King 1955). Had I collected data shortly after alarm call initiation, I likely would have detected an effect.

Distance from Colony Edge and Distance from Burrow

As predicted, prairie dogs foraged more alertly when nearer to the edge of the colony and farther from burrows. The edge of the colony is likely a risky foraging location because it is near the periphery of the group and near to predator concealment cover (Hoogland 1979, Fitzgibbon 1989). Foraging farther from refuge is more risky for an obvious reason - it takes longer to reach safety. Several studies have found a positive relationship between alertness and distance from safety (Holmes 1984, Carey and Moore 1986, but see Lima 1987). Prairie dogs likely forage more alertly when near to the colony periphery and farther from burrows because these are high-risk locations and they are sensitive to risk of predation when making foraging decisions.

Vegetation Height

Foraging prairie dogs did not increase their over all level of alertness when foraging in taller vegetation; however, they devoted more time to Upright alertness at the expense of Headbob alertness. Prairie dogs should adopt Upright postures when foraging in vegetation that is too high to view their surroundings from a Headbob posture. Carey and Moore (1986) found that Yellow-bellied marmots foraged more alertly when in areas of dense vegetation. Furthermore, Metcalfe (1984) reported that turnstones (Arenaria interpres) and purple sandpipers (Calidris maritima) foraged more alertly when among boulders that obstructed their view of their surroundings. The lack of a relationship between Veghigh and alertness in my data might result because the maximum height of vegetation that prairie dogs were observed in was limited. Had it been possible to monitor the behaviour of prairie dogs foraging in even taller vegetation two outcomes are possible: they might forage more alertly to compensate for their impaired field of vision (Underwood 1982) or, given the limited usefulness of vision in tall vegetation, they might forgo alertness altogether in order to minimize the time they spend foraging in a location that is presumably very risky (Lima 1987).

Group Size

The level of alertness of foraging prairie dogs was negatively correlated with the number of nearby adults. Individuals in larger groups may be less at risk to predators by several mechanisms that are dependent on group size (Bertram 1978, Pulliam and Caraco 1984) and may forage less alertly as a consequence. Documentation of a correlation between group size and individual alertness is voluminous. Elgar (1989) reviewed more than 70 papers that investigated the relationship between alertness and group size in more that 50 species of birds and mammals. My results are in agreement with most of these studies which report that individuals in larger groups forage less alertly.

The correlation between group size and alertness was strongest for the nearest measure of group size (<20m) and weakened considerably with increasing distance (Table 2 2). There are two candidate explanations for this observation.

First, nearer measures of group size might be better correlated with the number of individuals visible to foraging prairie dogs. Because an observer has an elevated vantage point, they may be able to see more individuals than a foraging prairie dog can. The visibility advantage of the observer likely increases with increasing distance from a foraging individual because at greater distances there is a greater chance that the line-of-sight between the forager and other prairie dogs is obstructed. Thus, alertness might be better correlated with nearer measures of group size because the forager's and observer's assessment of group size is more comparable.

Second, nearer group members might weigh more heavily in a foraging prairie dog's assessment of group size. Foragers should pay more attention to their immediate neighbours when assessing group size because most near individuals (especially those within 20m) are genetically related coterie mates (Hoogland 1983) who may be more likely to give warning call when they detect predators (Hoogland 1983). For other species of ground squirrels Sherman (1977) and Davis (1984) have shown that propensity of an individual to give an alarm call is dependent in part on the number of nearby related individuals that the call will benefit. Furthermore, near individuals might be more useful group mates because they are in a better position to detect predators that are an immediate threat to a foraging individual. Hence, prairie dogs might "trust" nearby individuals more than distant animals and, thus, might weight them more heavily when assessing group size.

My data also suggest that the composition of a group influences prairie dog foraging behaviour. Regardless of the distance-class of the measure of group size, alertness was not correlated with the number of pups in the vicinity of the forager. It would be wise for foraging adults to ignore young prairie dogs when assessing group size because pups are inexperienced and might be unreliable at detecting predators and giving alarm calls, two elements that are necessary in order for a forager to benefit from the presence of others. Robinson (1980) argued that young Belding's ground squirrels are unable to distinguish between predators and animals that pose no threat. Furthermore, because they can't differentiate between different types of alarm calls given by adults to ground and aerial predators (Robinson 1980), they presumably are unable to produce appropriate calls and thus would make less effective sentries. If the anti-predator behaviour of juvenile prairie dogs is similar to that of immature Belding's ground squirrels, foraging adults should not rely on them to detect predators and, hence, should not reduce alertness when foraging near to them.

Conclusion

I have identified a number of factors that possibly influence the level of alertness of foraging prairie dogs and have presented arguments that identify risk of predation as the likely mechanism by which these factors act. However, due to the correlative, exploratory nature of this study my conclusions are best treated as hypotheses for future consideration. In particular, my data suggest that hypotheses regarding the proximate mechanisms of group size assessment by foraging prairie dogs (who counts, which senses are involved, and how often is group size re-assessed) would be fruitful avenues of research.

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Table 2.1 Correlation coefficients (r) between 6 measures of behaviour and 14 environmental factors for six groups of prairie dogs. Sample sizes are 213, 286, 238, 262, 268, and 263 for groups 1-6 respectively. ("*" and "**" denote statistically significant correlation coefficients, p<0.05 and p<0.01 respectively.)

		MEASURE OF BEHAVIOUR					
FACTOR	GROUP	FEEDING			HEADBOB	UPRIGHT	VIGILANT
		%	#/min	ave.	%	%	%
WIND	1	-0.14*	0.06	-0.13	0.04	0.06	0.13
	2	0.11	0.07	-0.02	0.03	-0.15*	0.14*
	3	0.06	0.12	0.01	0.16*	-0.17**	0.08
	4	0.02	0.05	-0.08	0.10	-0.06	-0.08
	5	-0.11	0.12	-0.07	0.05	0.10	0.03
	6	0.04	0.05	-0.01	-0.03	0.02	-0.07
TEMP	1	0.09	-0.20**	0.07	-0.21**	0.00	0.02
	2	0.20**	0.16**	-0.02	0.19**	-0.27**	0.04
	3	0.04	-0.06	-0.02	-0.19**	0.04	0.07
	4	0.25	-0.14*	0.24**	-0.10	-0.21**	0.04
	5	0.08	-0.10	0.11	-0.09	0.00	-0.07
	6	0.08	-0.19**	0.16**	-0.09	-0.07	-0.10
CALLS	1	0.06	-0.03	-0.03	-0.05	-0.05	0.03
	2	0.06	0.07	0.01	-0.06	-0.05	-0.08
	3	0.01	-0.03	0.01	-0.11	0.07	-0.06
	4	-0.05	-0.01	-0.05	0.12	-0.03	0.06
	5	-0.09	0.17**	-0.14*	0.14*	0.04	-0.06
	6	-0.06	0.11	-0.06	0.09	0.03	-0.07

TABLE 2.1 (Cont.)

FACTOR	GROUP	FEEDING			HEADBOB	UPRIGHT	VIGILANT
		%	#/min	ave.	%	%	%
DISTCOL	1	-0.08	-0.05	0.08	0.05	0.01	0.12
	2	0.33**	-0.27**	0.29**	-0.04	-0.31**	0.07
	3	0.24**	0.00	0.15*	0.17**	-0.35**	0.07
	4	0.13*	-0.18**	0.19**	0.23**	-0.26**	-0.03
	5	0.04	-0.16**	0.14**	-0.01	-0.05	0.01
	6	0.03	-0.25**	0.18**	0.12	-0.13*	-0.05
DISTBUR[1]	1	-0.58	1.22	1.16	-0.07	0.64	-0.07
	2	-3.41++	1.57	-3.33++	-0.02	6.31++	0.47
	3	-0.66	0.73	-1.26	-1.36	1.45	-0.10
	4	0.95	2.94++	-1.56	0.13	-0.42	-2.08+
	5	-0.70	1.93	-1.49	0.68	0.51	-0.42
	6	-1.21	-1.12	0.17	-0.55	2.62++	-0.27
VEGHIGH[1]	1	0.77	2.24+	-2.52+	-0.06	-0.32	-1.44
	2	-3.84+	1.20	-3.49++	-2.07+	3.81++	0.96
	3	-3.06++	-1.27	-1.39	-1.68	3.66++	0.78
	4	1.93	-0.52	0.65	-2.87+	-1.09	0.50
	5	-1.76	-0.06	-1.70	-4.41++	3.35++	1.47
	6	0.31	-2.16+	1.45	-5.13++	3.33++	1.85

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[1] Data are test statistics of two-group T-tests performed on two classes of the factor.
+ = $p<0.05$, ++ = $p<0.01$.

TABLE 2.1 (Cont.)

MEASURE OF BEHAVIOUR

FACTOR	GROUP		FEEDING		HEADBOB	UPRIGHT	VIGILANT
		%	#/min	ave.	%	%	%
	1	0.13	-0.10	0.17*	-0.05	-0.04	-0.17*
	2	-0.08	-0.03	-0.01	0.07	0.05	0.00
TOTAL NEAR	3	0.16*	0.03	0.09	0.03	-0.17*	-0.02
	4	0.05	0.01	-0.02	0.11	-0.11	-0.02
	5	0.07	-0.01	-0.12	-0.01	-0.07	-0.06
	6	-0.02	-0.14*	-0.11	0.19**	-0.15*	-0.04
	1	0.19**	-0.11	0.22**	-0.07	-0.12	-0.09
	2	0.01	0.01	0.03	0.01	-0.02	0.03
NEAR ADULTS	3	0.28**	-0.06	0.20**	-0.06	-0.19**	-0.18**
	4	0.15*	-0.07	0.06	-0.01	-0.13*	-0.08
	5	0.09	0.03	-0.02	0.07	-0.13*	-0.13*
	6	0.13*	-0.08	0.12*	0.01	-0.10	-0.16*
	1	0.06	-0.06	0.10	-0.02	0.02	-0.16*
	2	-0.09	-0.04	-0.03	0.07	0.06	-0.02
NEAR PUPS	3	0.01	0.07	-0.02	0.07	-0.07	0.08
	4	0.00	0.04	-0.05	0.13*	-0.08	0.01
	5	0.04	-0.03	-0.01	-0.03	-0.03	-0.01
	6	-0.09	-0.13*	0.06	0.23**	-0.12*	0.03

TABLE 2.1 (Cont.)

		MEASURE OF BEHAVIOUR					
FACTOR	GROUP	FEEDING			HEADBOB	UPRIGHT	VIGILANT
		%	#/min	ave.	%	%	%
	1	0.18*	-0.17*	0.15*	-0.10	-0.05	-0.19**
	2	-0.06	0.21**	-0.13*	0.31**	-0.06	-0.01
TOTAL DISTANT	3	-0.11	0.15*	-0.10	0.15**	0.05	-0.06
	4	-0.10	0.12	-0.21**	0.09	0.06	-0.04
	5	0.09	0.01	-0.06	0.00	-0.09	-0.05
	6	0.10	-0.13*	0.14*	0.04	-0.14*	-0.08
	1	0.22**	-0.12	0.23**	-0.04	-0.15*	-0.11
	2	0.07	0.11	-0.01	0.14*	-0.10	-0.08
DISTANT ADULTS	3	-0.08	0.16**	-0.11	0.16**	0.05	-0.16**
	4	0.03	0.10	-0.08	0.03	-0.03	-0.04
	5	0.11	0.02	-0.02	-0.01	-0.08	-0.13*
	6	0.13*	-0.08	0.11	-0.06	-0.03	-0.15*
	1	0.11	-0.15*	0.06	-0.10	0.02	-0.19**
	2	-0.11	0.21**	-0.16**	0.31**	-0.2	0.03
DISTANT PUPS	3	-0.09	0.10	-0.07	0.11	0.03	0.03
	4	-0.15*	0.09	-0.23**	0.10	0.10	-0.02
	5	0.05	0.01	-0.05	0.00	-0.06	0.01
	6	0.05	-0.11	0.10	0.08	-0.15*	-0.01

TABLE 2.1 (Cont.)

MEASURE OF BEHAVIOUR

FACTOR	GROUP	FEEDING			HEADBOB	UPRIGHT	VIGILANT
		%	#/min	ave.	%	%	%
	1	0.14*	-0.05	0.04	-0.02	-0.10	0.04
	2	-0.01	-0.04	-0.02	0.06	-0.01	0.01
TOTAL COLONY	3	-0.04	0.10	-0.06	0.18**	-0.08	0.08
	4	-0.02	0.12*	-0.22**	0.11	-0.03	-0.02
	5	0.07	0.09	-0.12	0.06	-0.08	-0.18**
	6	0.16*	0.07	0.06	-0.02	-0.10	-0.17**
	1	0.19*	-0.03	0.12	0.00	-0.20**	0.04
	2	0.01	-0.01	-0.02	0.03	-0.01	-0.04
COLONY ADULTS	3	-0.01	0.05	0.00	0.14*	-0.07	0.01
	4	0.08	0.10	-0.08	0.03	-0.09	-0.03
	5	0.07	0.09	-0.12	0.07	-0.06	-0.22**
	6	0.16*	0.11	0.04	-0.04	-0.07	-0.18*
	1	0.07	-0.04	-0.03	-0.04	0.00	-0.13
	2	-0.02	-0.04	-0.02	0.06	-0.01	0.04
COLONY PUPS	3	-0.06	0.11	-0.08	0.16*	-0.07	0.11
	4	-0.08	0.09	-0.23**	0.11	0.01	0.00
	5	0.05	0.01	-0.05	0.00	-0.06	0.01
	6	0.05	-0.11	0.10	0.08	-0.15*	-0.01

TABLE 2.2 For 9 measures of group size, the fraction of all correlation coefficients that were greater than or equal to r=0.10 that suggested a negative relationship between alertness and the measure of group size. Measures of group size are presented as a matrix of three distance categories (<20m, <40m, colony) and three enumeration categories (adults, pups, and total). Data for each cell in the matrix was derived from a separate group size factor included in table 2.1.

DISTANCE CLASS	ADULTS	PUPS	TOTAL
	r>0.10	r>0.10	r>0.10
NEAR <20m	16/16	4/6	8/12
DISTANT <40m	12/18	7/17	9/17
COLONY	6/10	5/9	6/12

III. THE EFFECT OF GROUP SIZE ON THE FORAGING BEHAVIOUR OF BLACK-TAILED PRAIRIE DOGS (Rodentia: Cynomys ludovicianus): AN EXPERIMENTAL APPROACH

INTRODUCTION

Black-tailed prairie dogs (Cynomys ludovicianus) are diurnal, semi-fossorial rodents that inhabit short- and mixed-grass prairie habitats of the Great Basin region of central North America. They are of particular interest to sociobiologists because they live in dense colonies and possess a unique social system - colonies are composed of number of cohesive family groups that defend contiguous "coterie" territories. Each coterie typically contains one adult male, two to four adult females and ten to twenty yearlings and young-of-the-year (King 1955). Black-tailed prairie dogs ("prairie dogs" hereafter) are the most densely colonial and most socially integrated of all ground dwelling squirrels (Michener 1983, Armitage 1981).

A number of costs of group living have been identified. Of these, two may be universal (Alexander 1974): higher rates of parasite and disease transmission and greater competition for resources (such as food, space, or mates - see Hoogland, 1979a, for a discussion of the costs of prairie dog coloniality.) The fact that group living has associated costs begs the question, "why do prairie dogs live in colonies?"

If group living is adaptive it will evolve in a species because its benefits, in fitness terms, outweigh its costs. What then might be the advantages of prairie dog coloniality that have favoured its evolution?

Enhanced safety from predators is the most taxonomically widespread of the many proposed benefits of group living. Animals in groups may be less exposed to predators through a number of mechanisms - all of which increase in effectiveness as group size increases (Bertram 1978). Below I outline four such mechanisms that may operate in prairie dog colonies:

(a) **Enhanced predator detection** (Galton 1883, Hoogland 1981). The combined sensory systems of many are likely more effective than those of an individual at detecting approaching or concealed predators. Prairie dogs can benefit from the alertness of others and be less at risk to predators provided that individuals who first detect a predator in some way communicate their discovery to other group members.

(b) **Dilution** (Milinski 1977, Bertram 1978). Prairie dogs may be less at risk to predators when in groups because each individual is less likely to be selected by a predator when it is one of many potential targets. This general mechanism is known as predator swamping.

(c) **Confusion** (See refs. in Bertram 1978). Predators may be less successful when attacking groups of prey because they may be distracted by the seemingly haphazard movements of many fleeing targets.

(d) **Selfish herding** (Hamilton 1971). Prairie dogs in groups might further reduce their exposure to danger by selfishly positioning themselves at the centre of the group where they would be less likely to be the first individual encountered by an approaching predator, and hence, may be at less risk than peripheral individuals.

Prairie dogs are at risk to predators when foraging because they must leave the safety of their burrows to obtain food. Thus, foraging behaviour determines the degree to which prairie dogs satisfy two different fitness goals; maximizing energy intake and minimizing risk of predation. Commonly, individuals that are simultaneously predators and prey when foraging may be unable to maximise both safety and their rate of energy intake because behaviours that enhance one of these components of fitness are adopted at the expense of the other (Sih 1980). For example, a foraging prairie dog could minimize risk by continuously scanning its surroundings for signs of danger; however, extreme alertness is costly - alert individuals have less time to devote to feeding and would likely forage less efficiently as a consequence.

Foraging prairie dogs may benefit from group living by circumventing the aforementioned fitness tradeoff - by relying on the group for protection from predators, individuals can adopt highly profitable (risky) foraging behaviours yet expose themselves to no greater risk than they would experience when foraging alone. Thus, prairie dogs may benefit from group living **directly**, through enhanced predator avoidance, **indirectly**, through enhanced foraging efficiency, or, more likely, through a mixture of both.

Prairie dogs should benefit the most from a mixed strategy because returns to fitness from additional behavioral investment in either predator avoidance or foraging efficiency likely diminish as total returns from that component of fitness becomes maximized. Assume that individuals in groups benefit from a certain amount of additional predator avoidance. Beyond a point it would make sense for them to convert excess safety into enhanced foraging efficiency, where fitness returns might be more substantial. By the same token, individuals in groups should not convert all of their predator avoidance windfall to enhanced foraging efficiency because prairie dogs likely have digestive capacity and food processing rate limitations (Belovsky 1986) and it would be unrewarding for them to further sacrifice predator avoidance for enhanced foraging efficiency near or beyond this upper limit of food intake.

Prairie dogs can exchange safety for enhanced foraging efficiency in two ways:

(1) They can devote less time to alertness. Foraging prairie dogs periodically lift their heads and scan their surroundings, apparently, to look for predators. Feeding and scanning are at least partially incompatible behaviours - although individuals may process food while scanning, they are precluded from selecting new food items and sacrifice feeding time when in transition between postures (Elgar and Catterall 1981). Thus, less alert individuals likely forage more riskily but more efficiently than more alert individuals (Lima and Dill 1990).

(2) They can forage in high risk areas. The quantity and quality of forage in high risk areas is likely greater than that in low risk areas (Krueger 1986, Andrusiak and Harestad 1988, Devenport 1986) because, other things being equal, individuals will preferentially exploit low risk areas and deplete available food resources there (Ledger et al. 1983, Garrett et al. 1984). Thus, prairie dogs likely forage more efficiently when in risky locations because forage available in those areas is of higher quality.

Is enhanced foraging efficiency an advantage of group living? In a number of species, individuals devote less time to alertness and more to feeding when foraging in larger groups. Elgar (1989) recently reviewed studies that investigated the relationship between group size and predator vigilance in some 32 species of birds and 20 species of mammals. Of 74 studies, 66 reported a negative correlation between alertness and group size. However, because most of these studies were non-experimental and did not adequately control a number of potentially confounding factors, Elgar (1989) concluded that evidence for a causal relationship between group size and individual alertness was unconvincing and did not establish that individuals in groups **benefit** from enhanced foraging efficiency.

For example, in a correlational study of black- and white-tailed prairie dogs Hoogland (1979b) found a negative relationship between individual alertness and five measures of colony density. However, because this study was non-manipulative, prairie dog foraging behaviour may have been influenced not by colony density but by some other factor that was correlated with colony density. Thus, Hoogland's conclusion that reduced alertness is a **benefit** of prairie dog coloniality remains speculative.

Individuals in larger groups may also forage more efficiently by feeding in riskier (and potentially highly rewarding) locations. Devenport (1989) found that prairie dogs in larger groups foraged farther from their burrows than those in smaller groups. In other taxa individuals in large groups also forage in riskier places (Caraco et al. 1980). Again, because these studies are correlative, one cannot assess whether there is a causal relationship between group size and risky-place foraging. If group size **itself** influences the location of foraging sites, then risky-place foraging would be an advantage of group living. If some factor other than group size, competition for example, is responsible for differences in the location of foraging sites between large and small groups, then despite its correlation with group size, risky place foraging may not be an advantage of group living.

In this paper I present an experimental investigation of the relationship between group size and foraging behaviour in black-tailed prairie dogs. I chose an experimental approach to avoid some of the limitations of an observational study, with full knowledge that both experimental and observational approaches each have their strengths and weaknesses, and to gather data that will complement those collected in past studies.

Prairie dogs are excellent subjects for behavioral investigation. They are diurnal, forage in the open, can be readily captured and handled, and habituate well to observers and equipment. Furthermore, they are particularly suited to an experimental investigation of the advantages of group living for three reasons: (a) Prairie dogs are densely colonial. The advantages of group living are likely to be more apparent in a densely colonial species. (b) Prairie dog colonies are non-mobile and over the short term have a stable composition. The static nature of colonies allow particular individuals to be easily located and observed. In addition, the location of those individuals with respect to the rest of the group is less variable than with a species that forms mobile groups. (c) Prairie dog colonies are organized into a number of coterie territories. Coteries represent convenient units by which group size may be manipulated with a minimum of social disruption.

I addressed the question, "Is enhanced foraging efficiency an advantage of group living in black-tailed prairie dogs?", by determining the effect of group-size manipulations on prairie dog foraging behaviour. I predicted that prairie dogs in larger groups would forage more efficiently by:

1) **foraging less alertly** - prairie dogs can devote less total time to scanning their surroundings, by either decreasing the length of bouts of alertness, or by decreasing the frequency of interruptions of foraging.

2) **foraging in riskier locations** - prairie dogs can forage more riskily by foraging farther from burrows, nearer to the periphery of the colony, or in taller vegetation.

Group size manipulations were of two types - temporary and permanent. During a temporary manipulation I monitored the behaviour of selected individuals before and after their neighbours were removed from and subsequently reintroduced to the group. During permanent manipulations, group size was reduced and the foraging behaviour of the remaining individuals was monitored for a 3 - 4 week post-removal period. The intent of manipulations was to alter group size; however, prairie dogs might respond to manipulations not because group size was changed but because of uncontrolled effects of the experimental procedure or because the manipulation disrupted their cohesive social order. The main reason for conducting permanent manipulations was to evaluate alternate interpretations that predict a temporary rather than a permanent effect of group size manipulations.

MATERIALS AND METHODS

The Study Area

Prairie dogs were studied at Wind Cave National Park in southwestern South Dakota (43° 35' N latitude, 103° 25' E longitude, elev. 1100m - 1500m). The park lies on the south eastern edge of the Black Hills and straddles the ecotone of ponderosa pine forest (Pinus ponderosa) and northern mixed grass prairie. The park is home to bison (Bison bison), elk (Cervus elaphus), pronghorn (Antilocapra americana), and a number of terrestrial and aerial predators that pose a threat to prairie dogs (coyotes (Canis latrans), badgers (Taxidea taxus), bobcats (Felis rufus) ferruginous hawks (Buteo regalis), red-tailed hawks (Buteo jamaicensis), prairie falcons (Falco mexicanus), and bald eagles (Haliaetus leucocephalus)). See King (1955) for a more detailed description of the park.

Although protected within the park, prairie dogs are managed as a pest species and are controlled by poisoning and shooting. Colonies used in this study had not been managed in the previous four years.

Groups

Fourteen groups of prairie dogs were involved in this study. Groups were defined by the isolation of their members from other prairie dogs. Individuals in three of these groups were >2 km from other prairie dogs and were assumed to be completely isolated. The remaining 11 groups were peripheral fragments of larger colonies and were only partially isolated from nearby prairie dogs. Although individuals in the 11 peripheral groups were spatially separated from other prairie dogs (mean distance to nearest extra-group individuals = 85 m, range = 40 - 140 m) and for the most part were visually isolated as well (9 of 11 groups had fewer than 5 other prairie dogs visible within 200m), they were likely able to hear the vocalizations of hundreds of extra-group prairie dogs. Groups contained 10 - 58 adults and yearlings (mean = 25), 63 - 125 pups (mean = 63), and occupied an area of 0.6 - 3.5 ha (mean = 1.3 ha).

Trapping and Marking

Prairie dogs were captured in Tomahawk live traps (models 102, 103 and 104) that were baited with whole oats. Traps were distributed uniformly throughout the active area of a group at a density of 100/ha. Most were set within 1 - 2m of well used burrow entrances and, prior to intensive trapping, were wired open and filled with oats for 3 - 5 days to habituate prairie dogs to them.

The mass of captured prairie dogs was measured to the nearest 10 grams with a Pesola 1500g spring scale, their sex was recorded, and the width of their zygomatic arches was measured with plastic vernier calipers. Prairie dogs were given metal tags in both ears (National Band and Tag Co. style 1005-1) and an individually distinctive dye mark (Nyanzol A) on their fur. A saturated solution of water and Nyanzol A crystals was mixed 50:50 with Clairoxide (20 volume H_2O_2) at the marking site and was applied to the fur with a stiff-bristled, 1/2-inch-wide artist's brush.

Grids and Blinds

An observation blind and a grid of colour-coded, 24"-tall wooden stakes spaced 20m from one another were established on each group. On most groups low plywood walls (24" tall and 17' long) served as blinds; however, for three groups with no nearby vantage point, the observer was elevated 3m off the ground with two box-on-stilts blinds and one tree blind. When seated at any blind only the top half of an observer's head was visible from the perspective of a prairie dog. A t-shirt "scarecrow" was left flapping in the wind behind each blind to habituate prairie dogs to the silhouette and movements associated with the presence of an observer.

Preliminary Observations

Prairie dogs were further habituated to the presence of an observer during 3 - 5 three-hour-long observation sessions. During these periods observers monitored the interactions and movements of prairie dogs to determine the location of coterie boundaries and the coterie affiliation of individuals. One coterie in each group was designated a "focal coterie" on the basis of the following logistical criteria (ordered from most to least important): preferred coteries were, (a) entirely visible from the blind, (b) farthest from or best isolated from extra-group individuals, (c) located nearest to the centre of the group, and (d) contained between 4 and 6 adults. Focal coteries contained 3 - 9 adults (mean = 5.3), between 4 and 33 pups (mean = 12.3), were 0.13 - 0.46ha in size (mean = 0.30), and had a burrow entrance density of between 130 and 250/ha (mean = 190/ha).

Behavioral Observations

Behavioral data were collected during three-hour-long morning (7am - 11am) and evening (4pm - 8pm) observation sessions. During the summer months prairie dogs were most active at these times, spending more time in their cool burrows during the heat of the day (King 1955).

Foraging behaviour was quantified using "focal animal sampling" (Altmann 1974). The foraging behaviour of a selected individual was monitored for a predetermined period of time during which the time of initiation and termination of all bouts of behaviour were recorded.

Focal observations collected in 1989 were each five minutes long; however, upon comparing among-observation variation for observations of different lengths, I discovered that a duration of between 2 and 3 minutes minimized the standard error of a sample of observations (Appendix A). Thus, focal observations collected during the summer of 1990 were three minutes long. Fifteen five-minute-long or twenty three-minute-long focal observations could be collected during each three-hour-long watch session.

During each watch session an attempt was made to balance the number of observations collected on different focal animals. The individual who had been observed the fewest number of times during a particular session was preferentially selected as the subject of the next focal observation; however, data were collected from lower priority individuals if the highest priority individual was out of sight or not actively foraging when a focal observation was about to be initiated.

A focal observation was initiated only when a group was calm and the intended focal animal was actively foraging. It was interrupted in the event of a disturbance or if the focal animal for other reasons suspended foraging activities - periodically, foraging prairie dogs would run to or down burrows, engage in prolonged social interactions, or become alert for more than 10 seconds in an investigative manner. Interrupted observations were resumed if the group and focal animal returned to feeding within five minutes of the disturbance. If not, the observation was terminated at that point and another was initiated when the group eventually settled. Incomplete observations that were less than 2/3 the intended duration were discarded.

Prairie dogs were observed with the aid of tripod-mounted 10 x 50 wide angle binoculars. Foraging postures, non-foraging behaviours, and vocalizations were monitored and keyed directly into a Tandy 102 lap top computer as they occurred. An event recording program associated particular activities and occurrences with keys on the computer and produced a summary of each focal observation.

The following behaviours were monitored during focal observations:

a) foraging postures;

Feeding - spine parallel to the ground with head depressed more than 45° from horizontal.

Headbob - spine parallel to ground with head depressed less than 45° from horizontal **while chewing** or manipulating food.

Upright - standing/resting on haunches with both fore-legs off the ground **while chewing** or manipulating food. Spine usually inclined more than 45° from horizontal.

Alert - Headbob and Upright postures that do not involve chewing or manipulating food.

b) non-foraging behaviours;

Amicable - greeting, allo-grooming.
Agonistic - territorial disputes, tooth rattling, chasing.
Moving - walking with head up or loping for short distances.
Other - a catch all category including grooming, on mound, stretching, chasing insects.

c) vocalizations;

Jump-yip - the focal animal rears back, throws forelimbs and nose skyward, and emits a nasal, bark-like vocalization.
Jump-yip by Others - a jump-yip given by individuals in or near the group.
Alarm Call - a single alarm bark given by an individual in or near the group.
Repetitive Alarm Call - A rhythmic series of alarm calls that often persists for several
minutes. Given by individuals in or near the group.

Additional information was appended to each observation upon its completion: the identity of the observer, group, and focal animal; the month, date and time of day; the distance between the focal animal and the edge of the colony, the individuals distance from the nearest burrow, and the height of vegetation that it had been foraging in.

Group Size Manipulations

Group size was experimentally altered to determine what effect, if any, it has on the foraging behaviour of prairie dogs. Group size was reduced by live-trapping and removing designated individuals. Unfortunately, the complementary manipulation, group size enhancement, was not possible because prairie dogs would immediately disperse when introduced to an unfamiliar group (pers. obs.). However, group size enhancement was accomplished, in a fashion, by returning individuals that had been temporarily removed to their group of origin.

Group size manipulations were of two types: a) **temporary** - animals were removed, held in captivity, and were subsequently returned to the group, and b) **permanent** - removed animals were relocated to other colonies within the park.

In addition, manipulations were performed at two levels of intensity. "Maximal" treatments altered group size by removing or replacing all individuals not in the focal coterie and an average of 12.5 pups that were part of the focal coterie. An average of 4.2 adults and 1.0 pups remained in focal coteries during the reduced state of Maximal treatments. "Limited" treatments altered group size by removing or replacing all group members except those in the focal coterie. An average of 5.0 adults and 10.2 pups remained in the focal coterie during the reduced state of Limited treatments. Two of 4 Permanent and 4 of 8 Temporary manipulation groups received Maximal treatments. The remaining 6 groups received Limited treatments.

Temporary Manipulations

Temporary manipulations were conducted on eight different groups - four in each of the summers of 1989 and 1990. Each group was paired with another for the duration of the experiment. Behavioral data were collected simultaneously from both groups of a pair, and each group served as the other's "control" during their respective manipulation periods. Control groups were not true controls in the strict sense (Krebs et al. 1976). They served as reference groups that "controlled" for climatic and temporal effects on foraging behaviour; as well they provided a measure of the degree of stochastic variation in foraging behaviour against which the response of prairie dogs to experimental treatments could be compared. Removal and Replacement manipulations were conducted in sequence - first on one then on the other of a pair of groups. For each pair, the group that most quickly habituated to the presence of an observer was manipulated first.

The procedure of a Temporary manipulation was as follows: a) A baseline measure of foraging behaviour was established during a series of pre-removal observation sessions (3 sessions in 1989, 4 in 1990) for each group pair. b) Animals were live trapped and removed from one of the groups. Most of the animals targeted for removal were captured during the first session of the 1.5-day-long trapping period. c) Following the trapping period, three sessions of post-removal behavioral observations were conducted on both groups. Immediately after the third observation session captive animals were returned to the experimental group. Prairie dogs were held in captivity for at most 48 hours after the day of their capture. d) Groups were rested for 1.5 days, after which a post-replacement series of observations was conducted (3 focal sessions in 1989, 4 in 1990). The manipulation procedure was repeated; however, in this instance the former control group was manipulated while the former experimental group served as its control. This reciprocal manipulation procedure was carried out on each of four pairs of groups.

Permanent Manipulations

Eight groups were involved in Permanent removal experiments conducted during the summer of 1990. Four were designated as experimental groups and matched with a group that served as a permanent control. Behavioural observations were collected simultaneously from both groups of a Permanent removal pair. Because of a shortage of usable groups, two of the control groups used in this experiment had been part of Temporary manipulations conducted during the previous summer.

Baseline behavioral data were collected on alternate days for one week with two of the groups and for four weeks with two others. Designated animals were then removed from experimental groups and were relocated to areas 5 - 10 km away. Behavioral observations were periodically collected during an extended post-removal observation period. Two group pairs were followed for four weeks after the removal. Two others were observed for three weeks.

Treatment of the Data

Behavioral observations were culled and modified prior to statistical treatment.

A) Data from three focal animals in three groups were discarded because the observations collected from them were not adequately represented in all phases of the manipulation.

B) The frequency of all recorded **events**, was converted to the number of occurrences per minute of observation.

C) Three summary statistics (measures of behaviour) were calculated for all recorded **behaviours**: a) The number of bouts of the behaviour that occurred during each minute of observation, b) the average length of bouts of the behaviour, and c) the percentage of the total length of an observation that was devoted to the behaviour (note: the percentage of time devoted to Feeding, Headbob, Upright, and Alert behaviours was calculated as a portion of the total time devoted to these four behaviours, not the total length of the observation).

Because experimental treatments were applied at the level of the group, the group is the only statistically valid level of replication. However, in an attempt to reduce the amount of among- and within-group variability introduced by other factors, data were collected with many more layers of replication. More than one watch session was conducted during each pre- and post-treatment period for both Removal and Replacement manipulations. Furthermore, 15 - 20 observations were collected from several different Focal Animals during each watch session.

These additional levels of replication were collapsed in the following way. Means were calculated from observations pooled by both watch session and individual for each measure of behaviour. These sessional means were then pooled by manipulation period (pre- or post-removal, and, pre- or post-replacement) and a final weighted mean was calculated for each measure of behaviour. For this final calculation, sessional means determined from only one or two observations were weighted 1/3 and 2/3 as heavy as those calculated from three or more observations.

From the resulting grand means, the pre-to-post treatment change in each measure of behaviour was calculated for each group. For experimental groups this change represents the **response** of focal individuals to the treatment. For control groups this change represents "noise" or natural temporal variation in foraging behaviour.

To assess whether group size manipulations affect prairie dog foraging behaviour, the response of experimental groups must be evaluated with respect to changes that occurred in control groups over the same period of time. Henceforth, when the impact of a particular manipulation is discussed, I refer to the response of experimental groups adjusted for variation observed in control groups.

Statistical Analysis

All summary statistics and statistical analyses were produced with SAS version 6.0. The response of each measure of behaviour to the experimental **reduction** of group size was assessed by applying a paired T-test to a sample of 12 pairs of matched experimental and control groups. All tests were two-tailed and the level of significance was set at $\alpha=0.05$. Where the distribution of pair-wise, experimental-control group differences deviated significantly from normality (Shapiro-Wilk test, $\alpha=0.05$), a non-parametric Wilcoxon paired-sample test was substituted. Data for eight of the 12 group-pairs originated from the removal phase of Temporary manipulations. The remaining 4 pairs were Permanent manipulation groups. To make data from Permanent manipulation groups comparable to that from Temporary manipulation groups, all Permanent removal watch sessions not conducted within three days on either side of the trapping period were discarded prior to calculating pre- and post-removal period means.

The response of each measure of behaviour to experimental **enhancement** of group size was assessed using data from 8 pairs of experimental and control groups. Statistical tests were performed as described above. Data for all 8 group pairs were collected during the replacement phase of Temporary manipulations.

I compared the effects of Removal and Replacement treatments with paired t-tests (as described above). Data for this analysis were collected from eight temporary manipulation groups.

I compared the effect of Maximal and Limited treatments in both removal and replacement manipulations with two-group T-tests (two- tailed, α=0.05). Where the data failed assumptions of normality or equality of variance (F' statistic) a Mann-Whitney U test was substituted.

The data to which the above tests were applied, violates one or more statistical assumptions or principals of experimental design. First, there is a problem with non-independence - each of the eight groups involved in Temporary manipulation acted in both an experimental and control capacity over the course of the experiment. However, because the total number of suitable groups was limited and a considerable amount of time was invested in setting up equipment and trapping individuals on each, I thought it better to obtain a larger sample of manipulation responses than to cling religiously to the tenets of experimental design and commit half the groups at my disposal to serve as controls only.

Secondly, I have pooled data collected from different treatments, during different times of the summer, and in different years. In the strictest statistical sense, each subset should be treated as a separate experiment and analyzed independently. However, pooling across a number of treatments would tend to inflate among-group variation and would thus generate test results that would be statistically conservative.

RESULTS

Baseline Behaviours

None of the baseline behavioral measures differed statistically (two-group T-tests, all p>0.05) between experimental and control groups prior to Temporary or Permanent manipulations (Table 3.1). This result is not surprising for the temporary removal comparisons because the same 8 groups contributed data to both control and experimental samples.

Removal Experiment

As predicted, prairie dogs foraged more alertly, devoted less time to feeding, and foraged in less risky locations when the size of their groups were experimentally reduced (Figs. 3.1-3.4). The magnitude of behavioral changes between pre- and post-removal periods was highly variable among both experimental and control groups; however, most groups responded in the predicted direction for most measures of behaviour (Appendix B, Tables 1-4). There is a general trend for variation to be greater among experimental than among control groups (Figs. 3.1-3.4).

Despite this variation, the reduction (13% from baseline) of the proportion of time that prairie dogs in experimental groups devoted to Feeding was statistically significant (p=0.0004, Fig. 3.1). Because feeding periods were interrupted by longer and more frequent bouts of alertness, bouts of Feeding became 50% shorter (p=0.0002, Fig. 3.2) and 40% more numerous (p=0.0002, Fig. 3.3).

The proportion of time devoted to alert postures increased in experimental groups after the removal: Headbob by 36% (p=0.004), Upright by 25% (p=0.09), and Alert by 120% (p<0.001, Wilcoxon paired-sample test)(Fig. 3.1). The frequency of occurrence of all three increased - Headbob (43%, p=0.0002), Upright (44%, p=0.02), and Alert (170%, p<0.001, Wilcoxon paired-sample test)(Fig. 3.2) - as did the duration of bouts of Upright (11%, p=0.38) and Alert (33%, p=0.03)(Fig. 3.3). Surprisingly, the duration of bouts of Headbob **decreased** 15% from baseline (p=0.03, Fig. 3.3).

Focal animals in experimental groups interrupted the foraging period twice as often (p=0.0004) during the post-removal period. Furthermore, they tended to forage nearer to burrows (25%, p=0.16), farther from the edge of the colony (20%, p=0.15), and in shorter vegetation (6%, p=0.12)(Fig. 3.4).

Replacement Experiment

The response of prairie dogs to the replacement treatment was opposite in direction to that of the removal treatment for every measure of behaviour but "distance from edge of colony" (Fig. 3.5-3.8). When previously removed individuals were reintroduced, focal animals became less alert, devoted more time to feeding, and foraged in riskier locations. However, the behavioral response was highly variable and not statistically significant for most measures of behaviour. Furthermore, for all measures of behaviour a smaller proportion of groups responded in the direction predicted for replacement manipulations than for removal manipulations (Appendix B - Tables 1-8). There was a trend for the response of experimental groups to be more variable than that of control groups (Figs. 3.5-3.8).

Focal animals in experimental groups increased the proportion of time they devoted to head down Feeding (8% of the pre-**removal** baseline, p=0.15, Fig. 3.5). Because Feeding postures were less frequently interrupted after the removal, bouts of Feeding were 22% longer (p=0.10, Fig. 3.7) and 14% less numerous (p=0.13, Fig. 3.6).

Prairie dogs in experimental groups devoted less time to alert postures after replacement manipulations: Headbob (21%, p=0.19), Upright (10%, p=0.75), and Alert (100%, p<0.01, Wilcoxon paired-sample test)(Fig. 3.5). The reduction in the proportion of time devoted to these measures of alertness occurred in a different way for each: the frequency of bouts of Headbob decreased (23%, p=0.12), the duration of bouts of Upright decreased (16%, p=0.17), while both the frequency (100%, p=0.22) and duration (50%, p=0.001) of bouts of Alert decreased (Figs. 3.6 and 3.7) .

Prairie dogs in experimental groups interrupted foraging activities 95% less often (p=0.02) during the post-replacement period. As well they tended to feed farther from burrows (30%, p=0.16), but not nearer to the edge of the colony (2%, p=0.88), and in taller vegetation (3%, p=0.62)(Fig. 3.8).

Removal vs. Replacement Manipulations

Data from the eight Temporary manipulation groups was used to compare the relative effect of Removal and Replacement treatments on the foraging behaviour of prairie dogs. There was a trend for the impact of the replacement manipulation on the foraging behaviour of prairie dogs to be weaker (for 14 of 16 measures of behaviour) (Table 3.2) and more variable (for 13 of 16 measures of behaviour) than that of the removal manipulation (Figs 3.1-3.8). More specifically, for 11 of 16 measures of behaviour, the magnitude of response to the replacement manipulation was roughly two-thirds of that to the removal manipulation (Table 3.2). However, the magnitude of the response differed statistically for only two measures of behaviour; the change in the frequency of bouts of Feeding and Alert was greater for the removal manipulation.

Permanent Removal Experiment

For each of the four experimental and four control groups involved in this manipulation, I pooled all pre-removal observations and determined baseline values for all measures of behaviour. I grouped observations collected after the size of experimental groups was reduced into three periods; 0-7 days, 8-16 days, and 17+ days and again computed means for all measures of behaviour.

Focal animals in experimental groups foraged more alertly and in less risky locations after the removal than they did before it. Their response was immediate and, more importantly, was persistent (Figs. 3.9-3.13). As time progressed, there was a trend for prairie dogs in both experimental (8 of 16 measures of behaviour) and control groups (7 of 16 measures of behaviour) to forage more cautiously (Figs. 3.9-3.13). However, the **net** response (the difference between experimental and control groups) was stable or exhibited no directional trend over time.

Prairie dogs in experimental groups devoted less of their foraging time to head down Feeding both initially (15% from the pre-removal baseline) and three weeks after (18% less) group size was manipulated (Fig. 3.9). Because feeding periods were interrupted by longer and more frequent bouts of alertness, bouts of Feeding became shorter (58% wk. 1, 37% wk. 3, Fig. 3.11) and more numerous (44% wk. 1, 28% wk. 3, Fig. 3.10).

The proportion of time devoted to alert postures increased - Headbob (50% wk. 1, 31% wk. 3), Upright (62% wk. 1, 62% wk. 3), and Alert (106% wk. 1, 52% wk. 3)(Fig. 3.9) - as did their frequency of occurrence: Headbob (45% wk. 1, 70% wk. 3), Upright (59% wk. 1, 66% wk. 3), and Alert (96% wk. 1, 70% wk. 3)(Fig. 3.10). The average length of bouts of Upright (23% wk. 1, 41% wk. 3) and Alertness (11% wk. 1, 30% wk. 3) also increased (Fig. 3.11). The average bout length of Headbob initially **decreased** (20%), as it did following temporary group size reductions; however, by the third week it had unexpectedly **increased** to level 22% greater than baseline (Fig. 3.10).

Focal animals in experimental groups interrupted the foraging period 30% more frequently during the first week after the manipulation but only 2% more often by the third week (Fig. 3.12). They also foraged further from the periphery of the colony (17% wk. 1, 39% wk. 3, Fig. 3.13). Initially, prairie dogs foraged nearer to burrows (21%) and in shorter vegetation (5%) but by the third week were foraging farther from burrows (15%) and in taller vegetation (6%)(Figs. 3.12, 3.13).

Maximal vs. Limited Treatments

The response of prairie dogs to Maximal (n=6 groups) and Limited (n=6 groups) treatments of the **removal** manipulation did not differ statistically for any of the 12 measures of behaviour (Table 3.3); however, its was greater for the Maximal treatment for 13 of 16 measures of behaviour. The response of prairie dogs to Maximal (n=4) and Limited (n=4) treatments of the **replacement** manipulation differed for two of the 12 measures of behaviour. Prairie dogs exposed to the Maximal replacement treatment foraged in shorter vegetation (p=0.04) and nearer to burrows (p=0.02) than did those in the Limited treatment (Table 3.3). Furthermore, the response to the Maximal treatment was greater for 14 of 16 measures of behaviour. Because of small sample sizes, these analyses are conservative.

DISCUSSION

Prairie dogs responded to both removal and replacement manipulations in the **direction** predicted for nearly every measure of behaviour. The response to changes in group size was **immediate** (within 36 hours) and **persisted** for at least three weeks after the permanent removal treatment. A number of responses were statistically significant, indicating that non-random changes in the foraging behaviour of prairie dogs were induced by group size manipulations.

When in larger groups, prairie dogs foraged less alertly and in locations where they were more exposed to predators. Past studies found a negative correlation between alertness and group size in Cynomys (Hoogland 1979b) and a number of other taxa (birds and mammals, Elgar 1989 and references therein; fish, Magurran et al. 1985). Other studies found that individuals in larger groups foraged in riskier locations. Devenport (1989) reported that black-tailed prairie dogs foraged farther from burrows with seasonal increases in colony density. Similarly, Caraco et al. (1980) observed that flock size was positively correlated with distance from escape cover.

My data suggest that a causal relationship exists between group size and risky foraging and supports the often-cited, but largely speculative, conclusion that enhanced foraging efficiency is a **benefit** of group living in prairie dogs, given that the following three assumptions are valid.

a) The relationship between foraging behaviour and group size can be extrapolated to a group size of one.

Prairie dogs responded to removal manipulations that reduced group size to approximately five adult members. Evidence from previous studies suggests that they likely would have responded as strongly, if not more strongly, had groups been reduced to a lone individual. In several studies the slope of the relationship between group size and the level of individual alertness was found to be greatest beneath a group size of five (Powell 1974, Jarman 1978, Bertram 1980) and asymptotic beyond a group size of 10 (Lazarus 1979, Elgar and Catterall 1981, MacWhirter 1988).

b) Prairie dogs forage more efficiently when foraging more riskily.

There is no reliable way to directly measure the foraging efficiency of free-ranging prairie dogs. Despite this, both logic and indirect evidence suggest that prairie dogs should forage more efficiently when feeding less alertly and in riskier locations.

The trade-off between individual alertness and foraging efficiency seems straight forward - individuals who devote less time to alertness have more time available for foraging. However, during most bouts of alertness prairie dogs combine scanning with food item processing and thereby might adopt alert postures without a large sacrifice in foraging efficiency (Devenport 1986). Prairie dogs may make the best of sacrificed foraging time by processing food items during bouts of alertness, but for two reasons are likely unable to fully compensate for the associated reduction in foraging efficiency: a) foraging time is lost in the transition between postures, and b) when alert, prairie dogs may be unable to locate and acquire new food items.

Individuals that forage in riskier **locations** likely do so more efficiently because the forage available in those areas may be more abundant and of higher quality than is less risky areas. Other things being equal, prairie dogs should preferentially forage in less risky locations (Garret et al. 1984, Carey and Moore 1986), thereby depleting preferred forage in those areas. Past studies have found that the biomass and availability of preferred species of vegetation on ground squirrel colonies is greater in riskier locations (farther from burrows and nearer to the edge of the colony). Andrusiak and Harestad (1989) reported that juvenile and yearling Columbian ground squirrels (Spermophilus columbianus) foraged more efficiently when farther from burrows and attributed the difference to a greater abundance of preferred forage. Garrett et. al (1984) and Krueger (1986) found that the biomass of forage preferred by prairie dogs is greater near the periphery of a colony. Krueger (1986) also found that prairie dogs foraged more efficiently (their bite/step ratio was greater) at the periphery than near the centre of a colony.

c) Prairie dogs responded to manipulations because group-size was altered.

The removal and replacement of individuals may have affected group size, as assessed by foraging prairie dogs, through a number of mechanisms. Potential cues may have been visual (vegetation on colonies was usually short enough that animals could observe one another directly), auditory (alarm calls, jump-yips, etc.), social (territorial disputes), or may have been any other feature of a prairie dog's environment that was affected by the manipulation. In the "Alternate Interpretations" section I outline and assess the likelihood that one or several of these secondary effects may have mediated the response of prairie dogs to experimental treatments.

Among-Group Variation

The response of prairie dogs to removal and replacement manipulations was highly variable among groups for most measures of behaviour. Furthermore, variation tended to be greater among experimental groups than among control groups (Figs. 3.1-3.13). Several factors might account for this variability.

First, the foraging behaviour of prairie dogs was likely influenced by a number of factors that were not amenable to experimental control. If prairie dogs compromise risk and efficiency when foraging, changes in factors that affect either should be reflected in their foraging behaviour. I could not control foraging factors - prairie dogs foraged where and on whatever they desired. Devenport (1986) found that prairie dogs adopted different levels of alertness when feeding on two varieties of provisioned food demonstrating that food type can influence foraging behaviour (see also refs in Lima and Dill 1990). Furthermore, several intrinsic and extrinsic factors may influence an individual's likelihood of encountering, detecting, or escaping from predators, and thus may influence foraging behaviour: body condition, age, wind, temperature, light intensity, time of day, the occurrence of vocalizations, and the appearance of predators, are examples (King 1955, Lima and Dill 1990, see also Chapter II of this thesis).

A second possible source of variation stems from the fact that treatments were not, and in many ways could not be, fully standardized. Half the groups were exposed to Maximal and half to Limited treatments. Manipulations were conducted in different years and at different times of the season. Pre- and post-manipulation group size, the total number of individuals that were removed and replaced during manipulations, and the spatial arrangement of neighbouring animals around focal coteries all differed among replicate groups.

The response of groups to manipulations may be variable because foraging prairie dogs can compromise risk and efficiency in different ways. If prairie dogs are less at risk when in groups they have the <u>option</u> to accept the benefit directly as enhanced survival <u>or</u> convert all or part of it into enhanced foraging efficiency by adopting more profitable (but riskier) foraging behaviours. The possible ways that foragers might partition the benefit of group membership between these two fitness goals lie on a continuum with enhanced survival at one extreme and enhanced foraging efficiency at the other (Lima and Dill 1990). Among-group variation in the intensity of the response to changes in group size might be a consequence of each group having adopted a different mix of safety and foraging efficiency - the response of individuals who convert a large portion of their group-derived safety into enhanced foraging efficiency would be greater than that of individuals who accept the group's anti-predator advantage primarily in the form of enhanced safety.

Lastly, variation among groups in the response of a given measure of behaviour might be a consequence of the fact that prairie dogs can respond to group size manipulations by altering any of several components of their behaviour. For example, individuals in one group might forage more alertly by increasing the proportion of time devoted to Headbob while those in another group might respond to a manipulation by foraging nearer to burrows. Consequently, the response of a sample of groups might vary considerably for a given measure of behaviour despite the fact that the magnitude of the response across all behaviours might be similar among groups.

Together, these factors may account for much unexplained variation in the foraging behaviour of prairie dogs. The influence of these factors do not bias the data; rather, it reduces the likelihood that the effect of a manipulation is statistically significant. The fact that, despite this variation, the response of a number of behaviours was statistically significant, further strengthens my conclusion that manipulations of group size influenced the foraging behaviour of prairie dogs.

Alternate Interpretations

I have concluded that there is a causal relationship between group size and the foraging behaviour of prairie dogs and have suggested that individuals in larger groups may benefit from enhanced foraging efficiency. However, my manipulations may have affected foraging behaviour for reasons that have nothing to do with group size or risk of predation. The increased alertness of individuals in small groups may be a compensatory response by foraging prairie dogs to some unexpected cost associated with removal manipulations - if so, enhanced foraging would not be a benefit of group living. Below, I outline and assess the validity of several alternate interpretations.

a) Observer Bias.

Because observers were not "blind" to experimental treatments their expectation of how manipulations would effect the behaviour of foraging prairie dogs may have influenced the data they collected. I have no way of assessing the contribution of observer bias to the outcome of my experiments. One argument against this alternate explanation, though a weak one, is that one might expect the magnitude of responses to be more similar than that observed if the treatment effect were solely an artifact of observer bias.

b) Procedure Effect.

Because sham manipulations were not conducted on control groups, the behavioral response of prairie dogs to experimental treatments may have been a "procedural effect". In the course of removal manipulations, observers disturbed groups to check traps and collect captured animals. Also, focal animals had access to oats and were often captured during trapping sessions.

Two lines of evidence argue against this "procedure effect" hypothesis. First, the hypothesis is inconsistent with the results of the Permanent Removal experiment - a procedure effect would likely not influence foraging behaviour for more than a few days, yet, the impact of the Permanent Removal persisted for at least three weeks (Figs. 3.9 - 3.13). Secondly, the disturbance associated with the Replacement manipulation was minimal (animals were simply set free), yet the response of prairie dogs to this treatment was substantial and in an **opposite** direction to that predicted by the "procedure effect" hypothesis.

c) Social Disruption.

Even though I conducted manipulations of group size in a manner that minimized disruption of the focal coterie, the social milieu of focal animals was affected when neighbouring individuals were removed. The disruption of the prairie dog's highly integrated social system by group size manipulations may have affected foraging behaviour in a number of ways: a) during periods of reduced group size, prairie dogs, for whatever reason, might be "looking" for their missing neighbours when foraging (Underwood 1982), b) prairie dogs likely become habituated to the presence of nearby individuals and might approach their novel post-removal social milieu as they do every novel stimuli - with caution (King 1955). c) during the post removal period, prairie dogs were free to move beyond the former boundaries of their coterie territories where they might forage more cautiously for two reasons: they would be unfamiliar with the location of forage and burrow entrances, and while trespassing on a neighbouring territory they might anticipate an aggressive encounter (King 1955).

All three of these mechanisms are dependent upon the **novelty** of the group size reduction. Over what time period should one expect the novelty of the manipulation to persist? One week? One month? One year? Because there are no natural social disruptions of comparable magnitude to compare my data to, I can only speculate. It seems reasonable to expect that if the novelty of the manipulation had not been lost within 1 - 2 weeks, it should have at least begun to diminish by this time. The outcome of Permanent removal manipulations suggest, if anything, that the magnitude of response **increased** during the 3 - 4 week post-removal period. Thus, with caution, I conclude that it is unlikely that prairie dogs responded to manipulations because their social milieu was disrupted.

d) Enhanced Success of Predators.

Prairie dogs may have foraged more conservatively after group size manipulations because they associated the disappearance of neighbouring individuals with increased predation intensity. If this were the case, one would expect the response of prairie dogs to diminish as time passes after the "predation" event. Because the effect of permanent group size manipulations did not decay over time, my data argue against this "enhanced predator success" interpretation.

e) Forage Quality Hypothesis.

Lastly, prairie dogs may have foraged less riskily when group size was reduced because the quality and availability of forage increased - prairie dogs likely can forage more conservatively and still acquire adequate nutrition when feeding on high quality forage. Forage quality is one of the main factors confounding past observational studies of the relationship between group size and foraging behaviour (Elgar 1989). Forage quality may have differed between pre- and post-manipulation periods because prairie dogs density, and hence foraging pressure, was altered. Manipulations altered prairie dog density in two ways; individuals were able to forage beyond the boundaries of their home coteries during removal periods, and, during Maximal removal manipulations the actual number of coterie members was reduced. Forage quality may have been greater during removal periods because each individual had access to more square meters of prairie - the **total** amount of primary production available to each would be greater, and the **density** of vegetation might increase in response to reduced foraging pressure.

The fact that the response of prairie dogs to Maximal and Limited treatments did not differ argues against the "vegetation quality" hypothesis. The hypothesis predicts that the response to the two treatments should differ because the change in density associated with the Maximal treatment was greater than that associated with Limited treatments. Furthermore, the response of prairie dogs to manipulations was immediate (within 36 hours), likely too soon for the density of the vegetation to have responded to the relaxation of foraging pressure.

Of the five alternate explanations discussed, the vegetation quality hypothesis is least refutable. My attempts to discredit it and other alternates is dependent largely on data from the Permanent Removal experiment and on comparisons of the Maximal and Limited treatments for which sample sizes are limited (n=4 and n=6 respectively).

Conclusions

To summarize, my data indicate that prairie dogs responded behaviourally to group-size manipulations. I have argued that this suggests that group size and foraging behaviour are causally related and have concluded that, for prairie dogs, enhanced foraging efficiency is a benefit of group living. My results support those of an earlier study by Hoogland (1979). Despite having stronger evidence for a foraging efficiency advantage of group living, I will not go as far as Hoogland (1981) and conclude that this and related predator avoidance benefits are the most important benefits that favoured the evolution of prairie dog coloniality. Whether enhanced foraging efficiency favoured the evolution of group living in prairie dogs and other ground dwelling squirrels, or whether group living evolved for other reasons and enhanced foraging efficiency is merely a secondary adaptation, an evolutionary fine tuning of the system, remains a matter of speculation.

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TABLE 3.1 Mean baseline behavioral measures of experimental and control groups prior to Temporary and Permanent Removal manipulations.

		TEMPORARY REMOVAL (n=8)		PERMANENT REMOVAL (n=4)	
		EXPT.	CONT.	EXPT.	CONT.
FEEDING	% of time	74.8	70.7	79.3	73.2
	#/min	6.0	6.8	5.7	6.1
	duration	9.2	8.0	10.4	9.7
HEADBOB	% of time	11.4	11.9	10.1	10.1
	#/min	4.5	4.8	4.3	4.2
	duration	1.6	1.5	1.5	1.5
UPRIGHT	% of time	11.4	14.8	8.4	14.0
	#/min	1.3	1.9	1.2	1.9
	duration	4.5	4.8	3.6	4.5
ALERT	% of time	2.4	2.7	2.2	2.1
	#/min	0.25	0.32	0.25	0.22
	duration	2.5	2.4	2.2	1.7
FREQUENCY OF FORAGING PERIOD INTERRUPTIONS (#/min)		0.17	0.18	0.25	0.21
PERCENTAGE OF FORAGERS WITHIN 2m OF A BURROW (%)		21.5	22.9	28.5	26.2
DISTANCE TO EDGE OF COLONY (m)		16.3	18.1	21.5	23.7
HEIGHT OF VEGETATION FORAGED IN (categoric units)		1.2	1.2	1.3	1.3

TABLE 3.2 The response for 16 measures of behaviour to Removal and Replacement treatments for 8 Temporary Manipulation groups.

		REMOVAL MEAN (n=8)	REPLACEMENT MEAN (n=8)	MEAN ABSOLUTE DIFFERENCE[1] (n=8)	p
	% of time	-8.2	5.9	2.3	0.45
FEEDING	#/min	2.2	-1.3	0.92	0.05
	duration	-3.6	2.1	1.5	0.27
	% of time	3.9	-2.4	1.5	0.28
HEADBOB	#/min	1.7	-1.0	0.65	0.13
	duration	-0.25	0.14	0.10	0.28
	% of time	1.5	-1.1	0.43	0.90
UPRIGHT	#/min	0.45	-0.02	0.43	0.47
	duration	0.30	-0.73	0.43	0.19
	% of time	2.7	-2.4	0.34	0.42
ALERT	#/min	0.44	-0.26	0.18	0.02
	duration	1.1	-1.4	0.24	0.59
FREQUENCY OF FORAGING PERIOD INTERRUPTIONS (#/min)		0.20	-0.16	0.04	0.25
PERCENTAGE OF FORAGERS WITHIN 2m OF A BURROW (%)		8.8	-6.3	2.5	0.32
DISTANCE TO EDGE OF COLONY (m)		1.3	0.38	1.7	0.68
HEIGHT OF VEGETATION FORAGED IN (categoric units)		-0.06	0.04	0.02	0.85

[1] removal and replacement responses added if in the same direction.

TABLE 3.3 Comparison of Maximal and Limited treatments for both removal and replacement manipulations.

		REMOVAL			REPLACEMENT		
		Maximal n=6	Limited n=6	p	Maximal n=4	Limited n=4	p
FEEDING	% of time	-10.3	-9.6	>0.05[1]	12.2	-0.4	0.08
	#/min	2.5	2.3	0.20	-1.6	-1.0	0.71
	duration	-5.2	-3.9	>0.05[1]	3.3	0.8	0.29
HEADBOB	% of time	4.2	4.1	>0.05[1]	-2.7	-2.1	0.89
	#/min	2.3	1.6	0.38	-1.3	-0.82	0.74
	duration	-0.33	-0.16	0.45	0.21	0.08	0.67
UPRIGHT	% of time	2.5	3.2	0.86	-5.8	3.6	0.17
	#/min	0.31	0.88	0.20	-0.35	0.31	0.53
	duration	0.37	0.66	0.81	-0.94	-0.51	0.69
ALERT	% of time	3.5	2.3	0.45	-3.8	-1.0	0.15
	#/min	0.53	0.31	0.33	-0.55	0.03	0.15
	duration	0.93	0.80	0.87	-1.5	-1.3	0.72
FREQUENCY OF FORAGING PERIOD INTERRUPTIONS (#/min)		0.20	0.14	0.39	-0.09	-0.22	0.24
PERCENTAGE OF FORAGERS WITHIN 2m OF A BURROW (%)		8.5	2.4	0.44	-14.6	2.1	0.02
DISTANCE TO EDGE OF COLONY (m)		6.2	0.3	0.18*	4.3	-3.5	0.18
HEIGHT OF VEGETATION FORAGED IN (categoric units)		-0.12	-0.04	0.41	-0.11	0.19	0.04

[1] Mann-Whitney U test

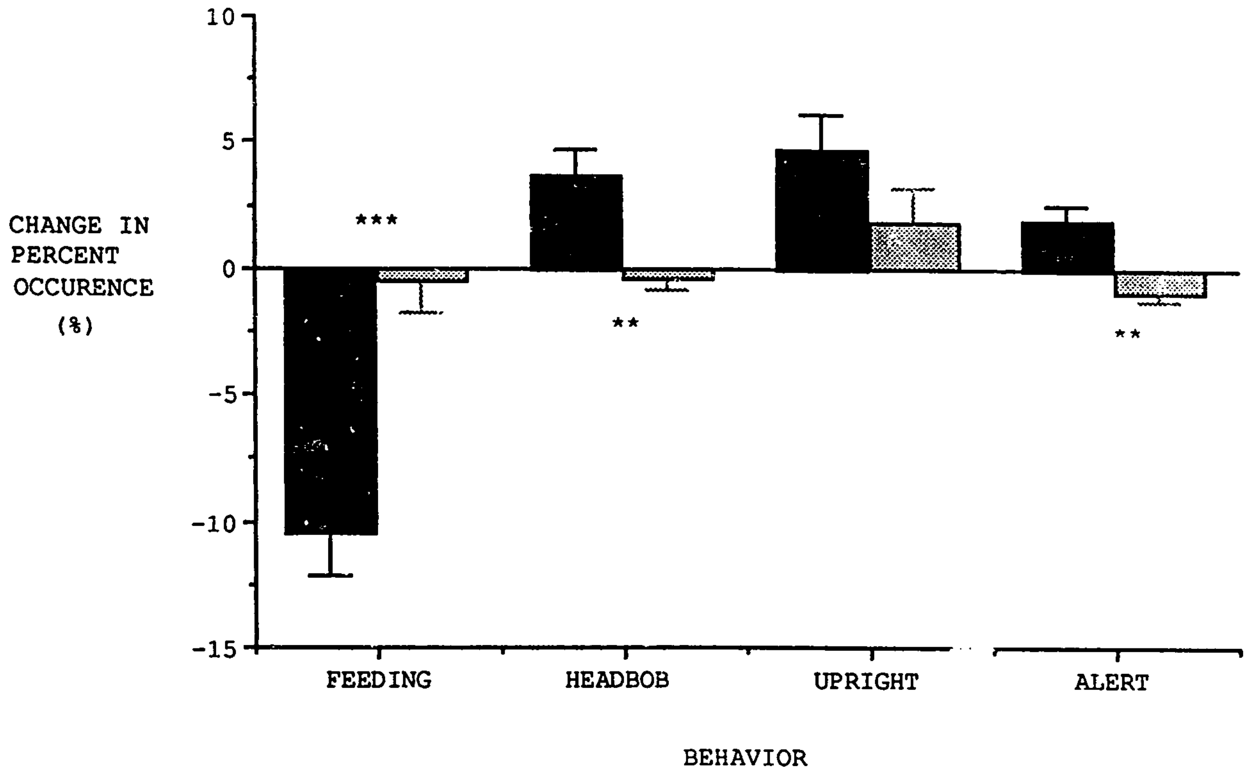


Figure 3.1 Mean (with SE bar) pre- to post- removal change in the percent of total foraging time that prairie dogs in 12 experimental (solid) and 12 control (stipple) groups devoted to Feeding, Headbob, Upright, and Alert (* = p<0.05, ** = p<0.01, *** = p<0.001)

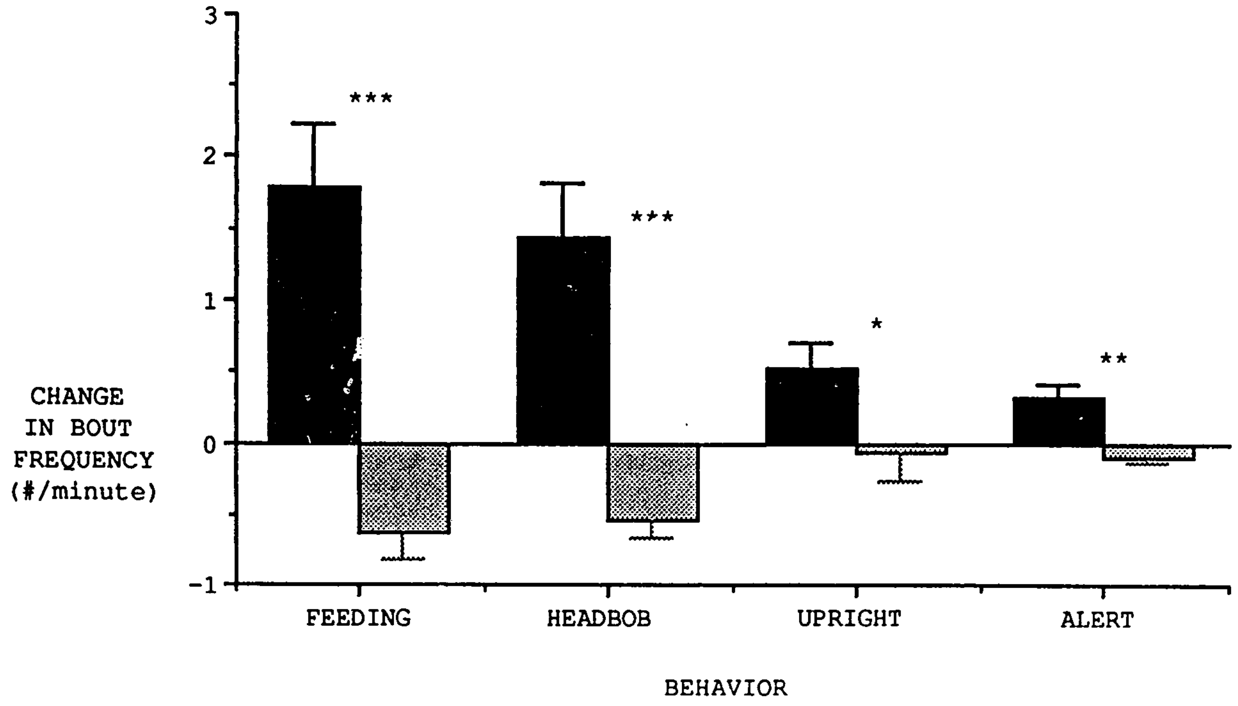


Figure 3.2 Mean (with SE bar) pre- to post- removal change in the frequency of occurrence of Feeding, Headbob, Upright, and Alert postures for prairie dogs in 12 experimental (solid) and 12 control (stipple) groups.
(* = p<0.05, ** = p<0.01, *** = p<0.001)

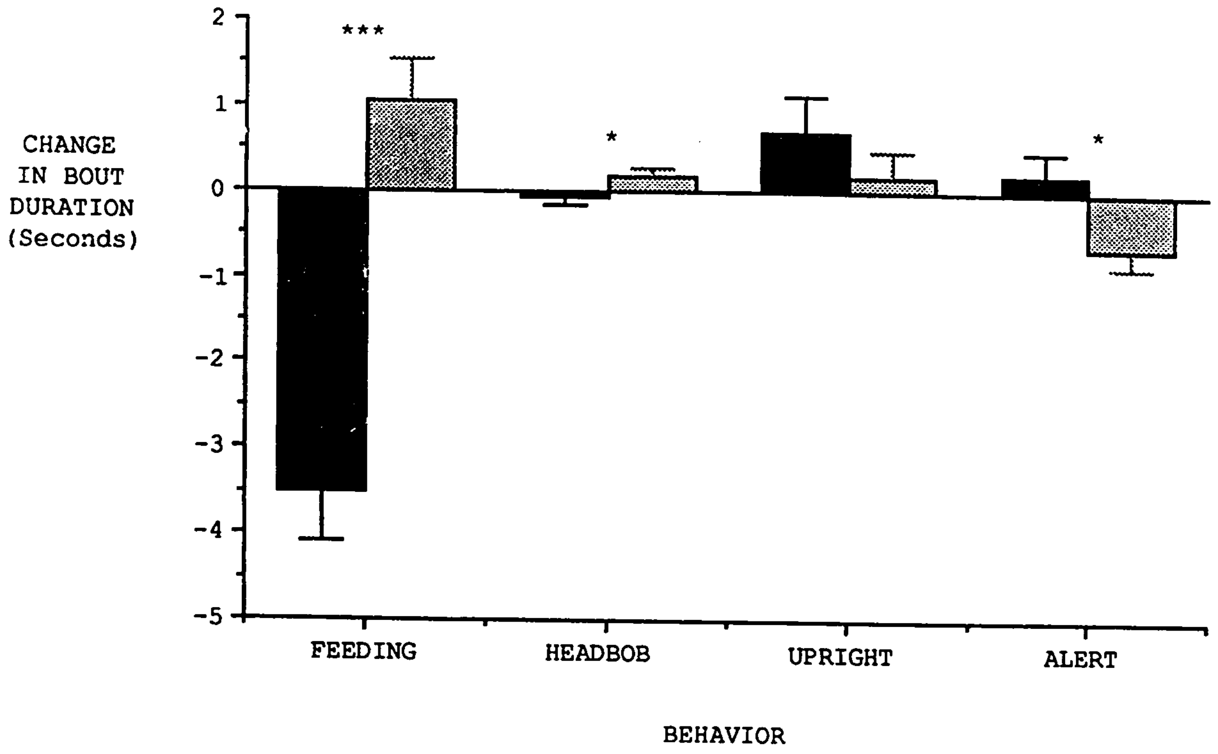


Figure 3.3 Mean (with SE bar) pre- to post- removal change in the average duration of Feeding, Headbob, Upright, and Alert postures for prairie dogs in 12 experimental (solid) and 12 control (stipple) groups.
(* = p<0.05, ** = p<0.01, *** = p<0.001)

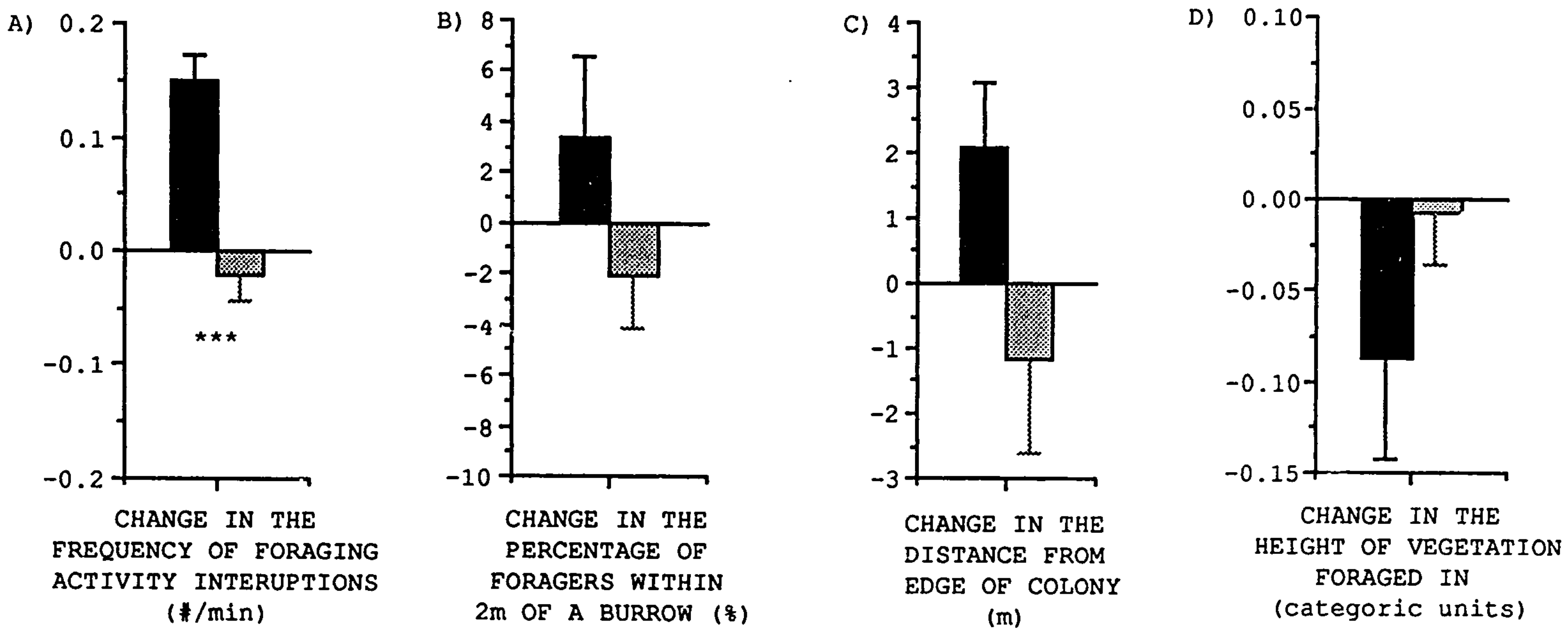


Figure 3.4 Mean (with SE bar) pre- to post- removal change in the four measured factors for prairie dogs in 12 experimental (solid) and 12 control (stipple) groups. (* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$)

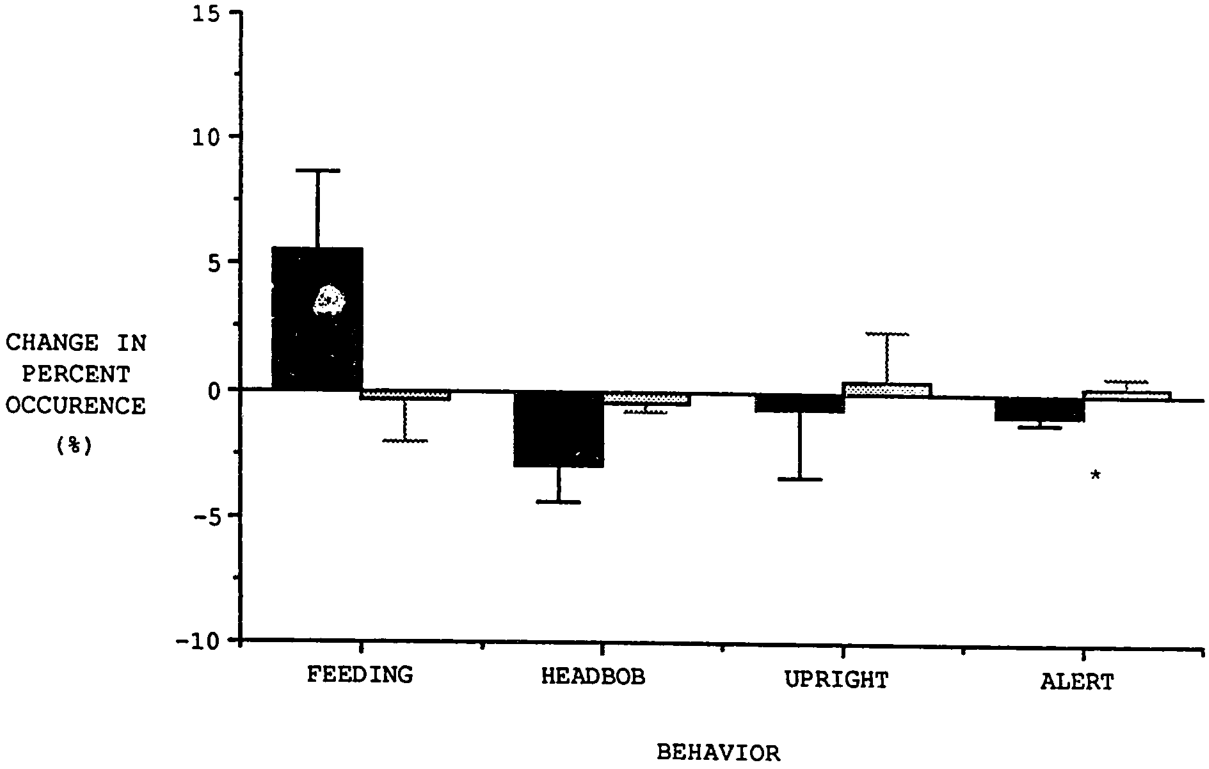


Figure 3.5 Mean (with SE bar) pre- to post- replacement change in the percent of total foraging time that prairie dogs in 8 experimental (solid) and 8 control (stipple) groups devoted to Feeding, Headbob, Upright, and Alert. (* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$)

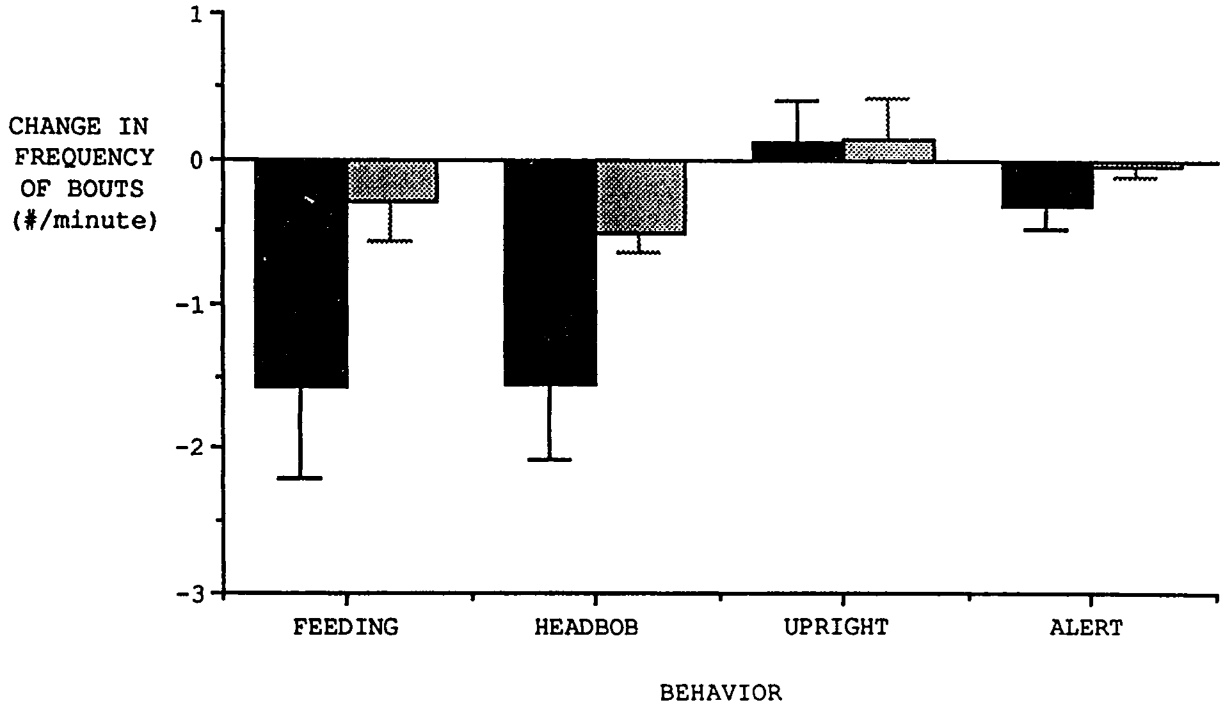


Figure 3.6 Mean (with SE bar) pre- to post- replacement change in the frequency of occurrence of Feeding, Headbob, Upright, and Alert postures for prairie dogs in 8 experimental (solid) and 8 control (stipple) groups.
(* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$)

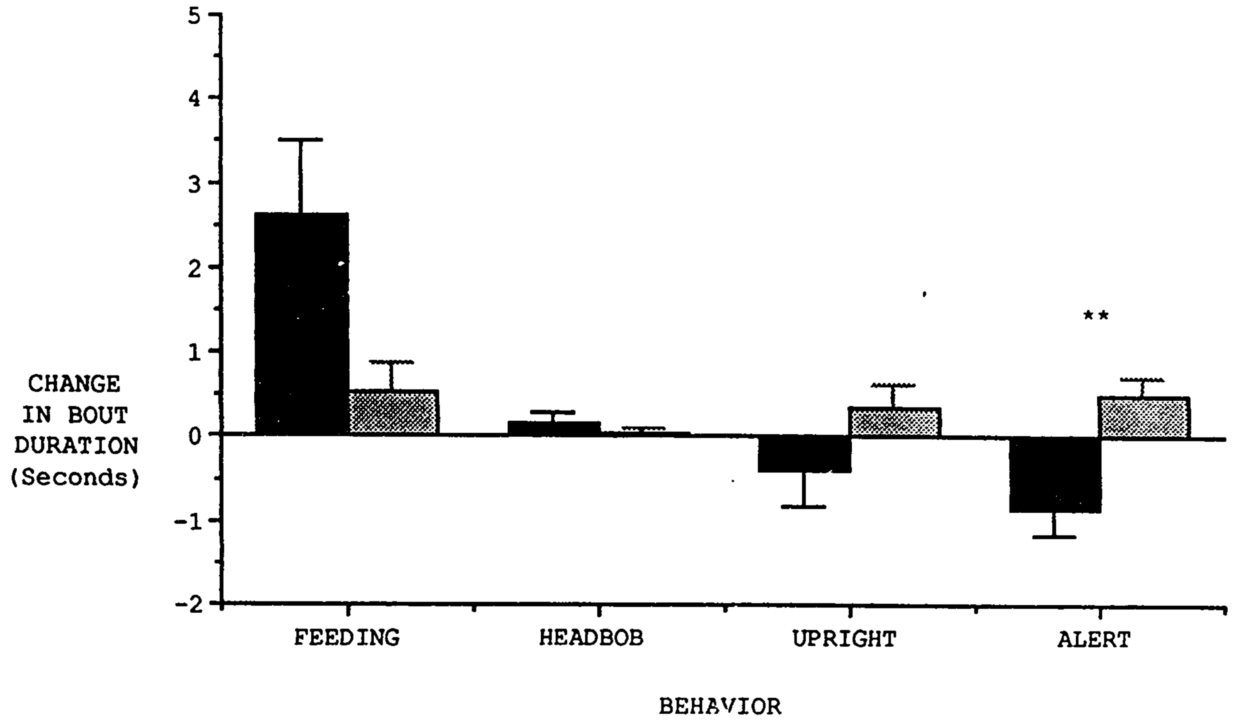


Figure 3.7 Mean (with SE bar) pre- to post- replacement change in the duration of bouts of Feeding, Headbob, Upright, and Alert postures for prairie dogs in 8 experimental (solid) and 8 control (stipple) groups.
(* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$)

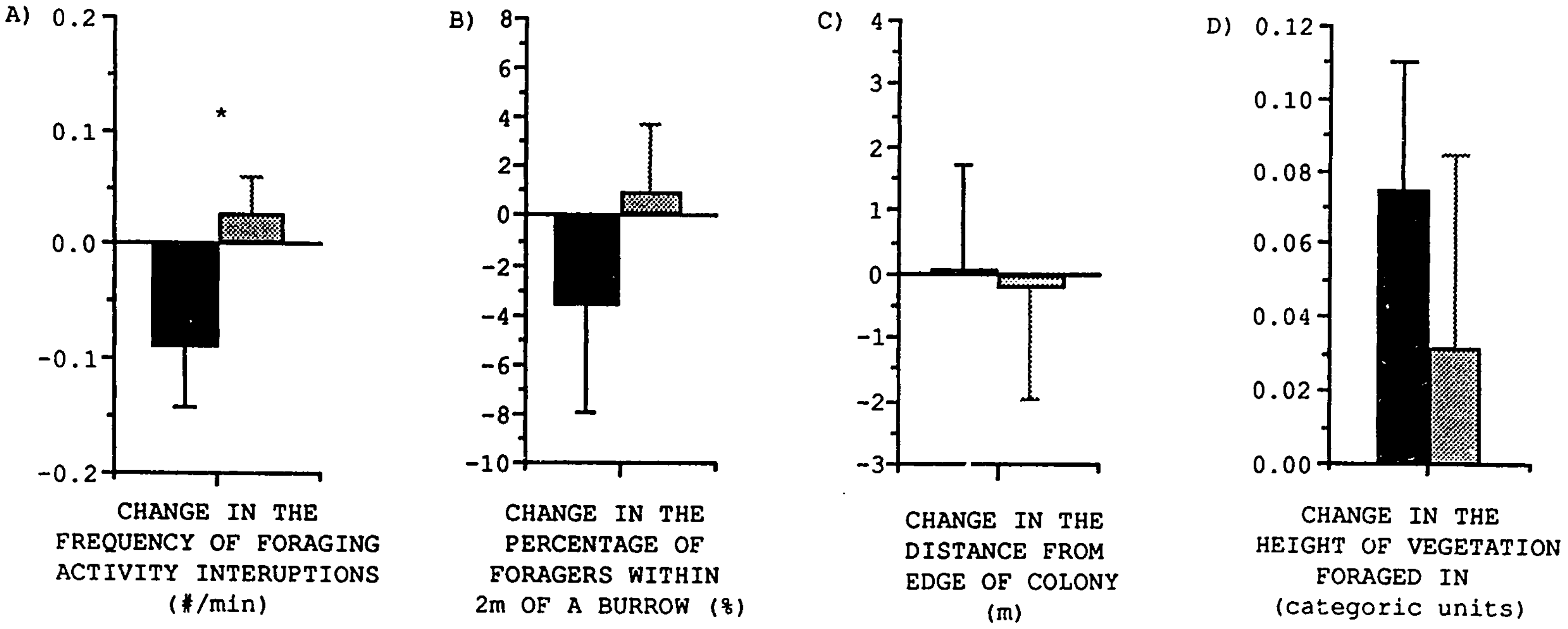


Figure 3.8 Mean (with SE bar) pre- to post- replacement change in the four measured factors for prairie dogs in 8 experimental (solid) and 8 control (stipple) groups. (* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$)

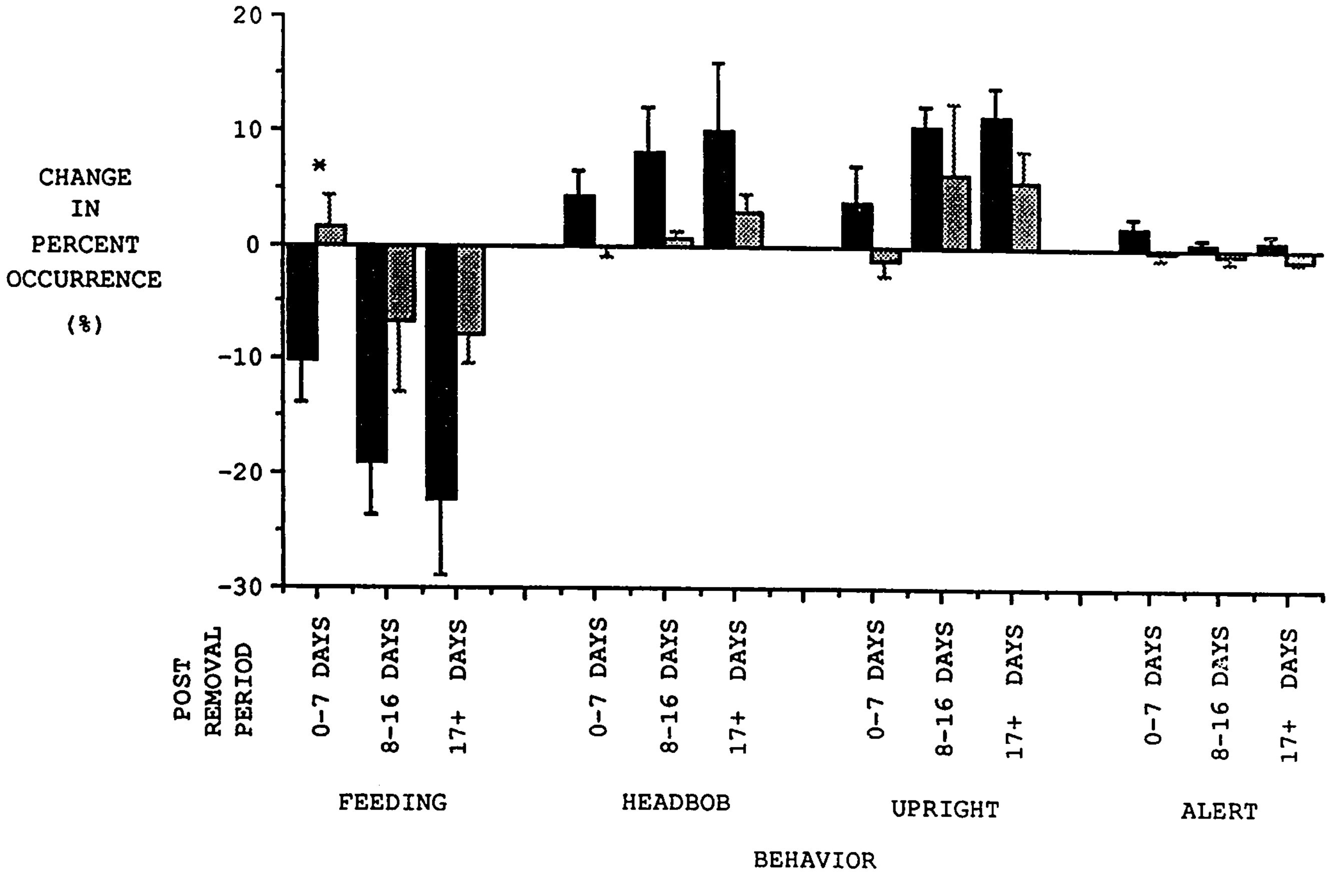


Figure 3.9 Mean (with SE bar) pre- to post- removal change in the percent of total foraging time that prairie dogs in 4 experimental (solid) and 4 control (stipple) groups devoted to Feeding, Headbob, Upright, and Alert during three post-removal periods.
(* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$)

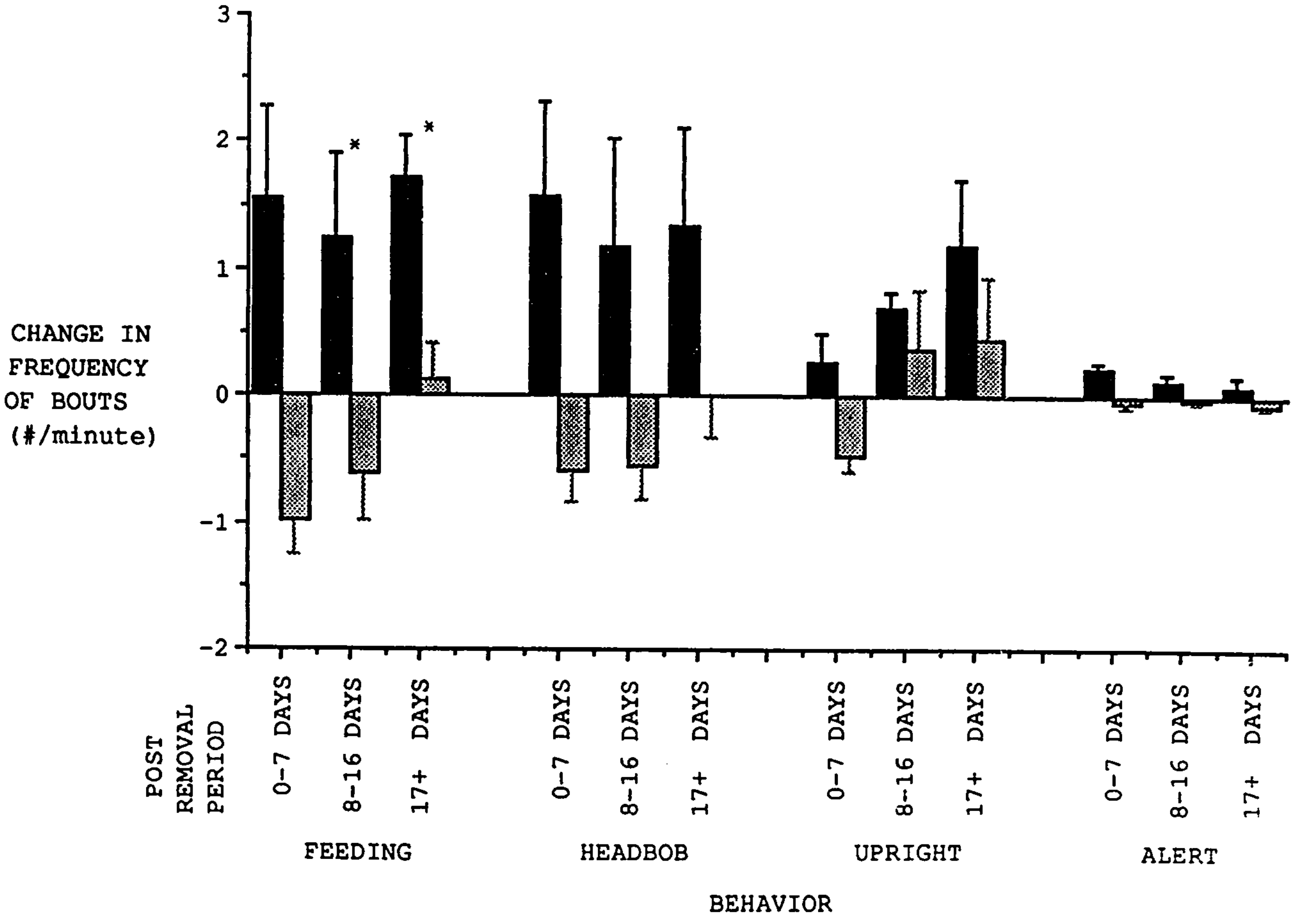


Figure 3.10 Mean (with SE bar) pre- to post- removal change in the frequency of occurrence of Feeding, Headbob, Upright, and Alert postures for prairie dogs in 4 experimental (solid) and 4 control (stipple) groups during 3 post-removal periods. (* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$)

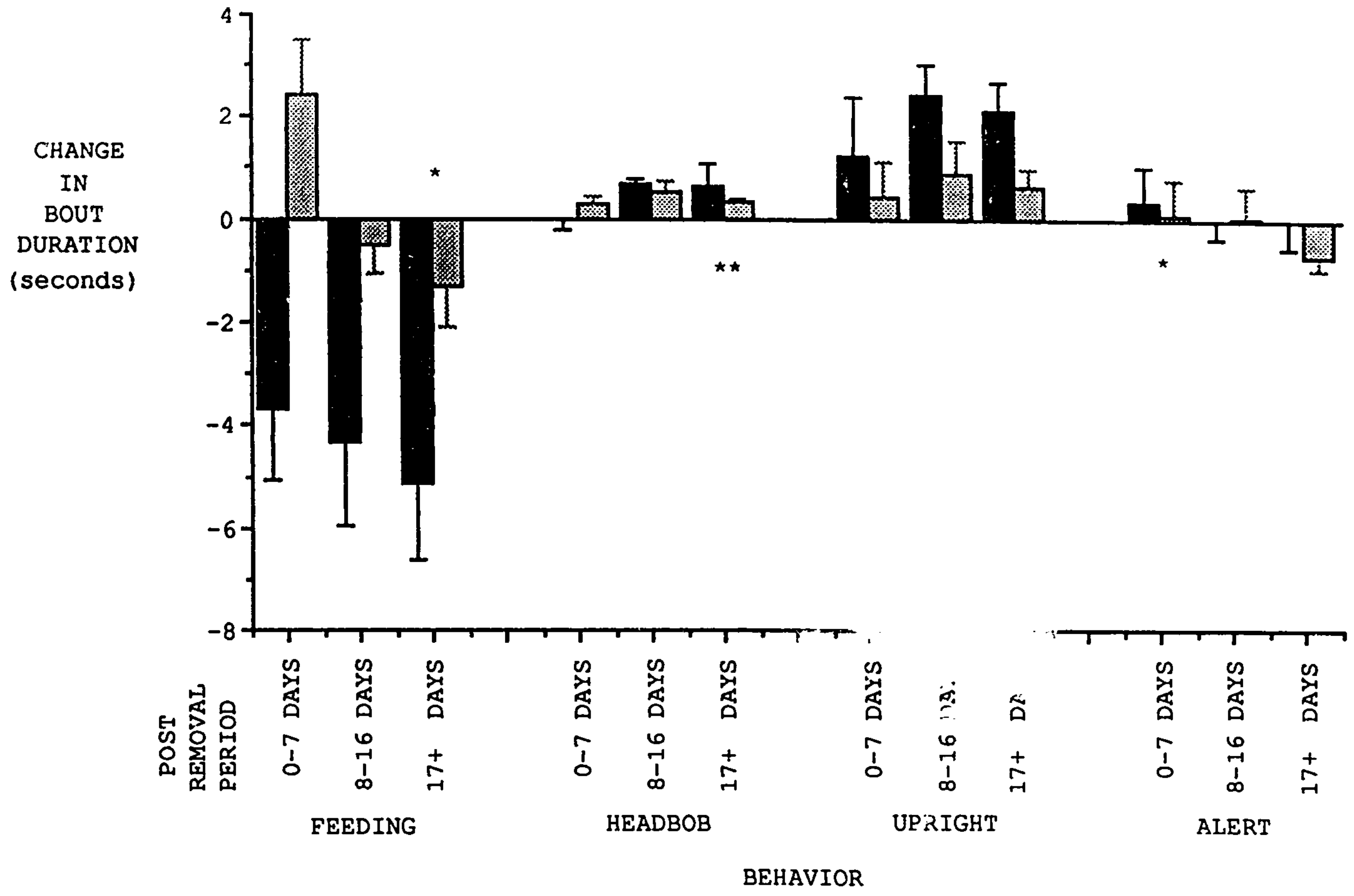


Figure 3.11 Mean (with SE bar) pre- to post- removal change in the duration of Feeding, Headbob, Upright, and Alert postures for prairie dogs in 4 experimental (solid) and 4 control (stipple) groups during 3 post-removal periods. (* = p<0.05, ** = p<0.01, *** = p<0.001)

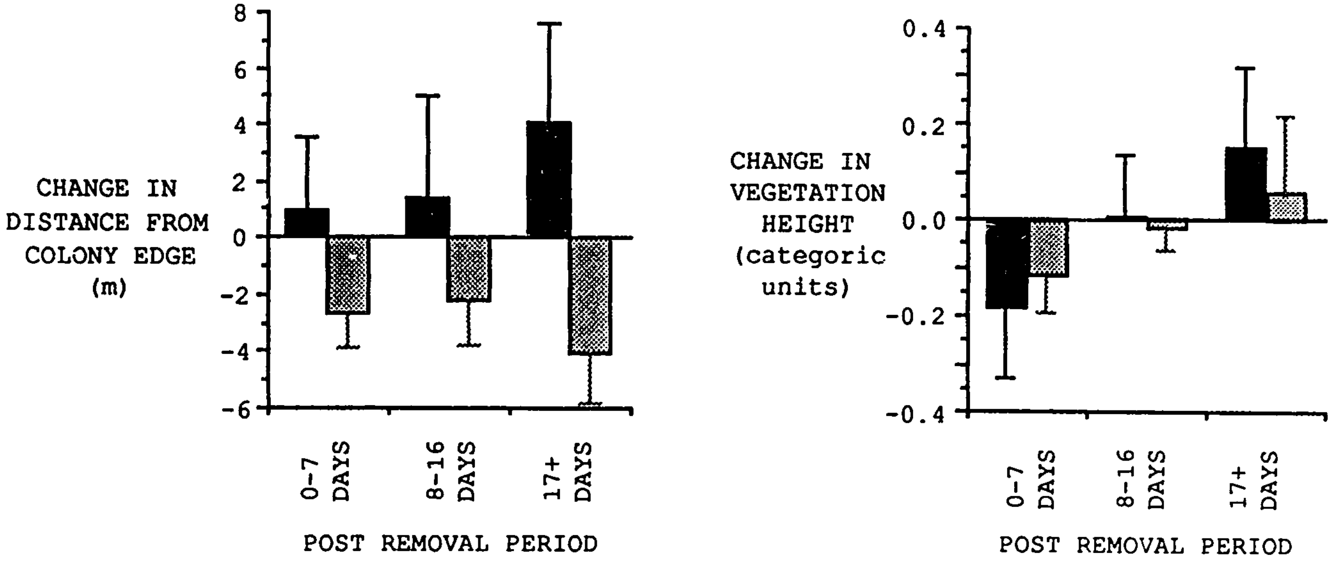


Figure 3.13 Mean (with SE bar) pre- to post- removal change in two factors for prairie dogs in 8 experimental (solid) and 8 control (stipple) groups during 3 post-removal periods. (* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$)

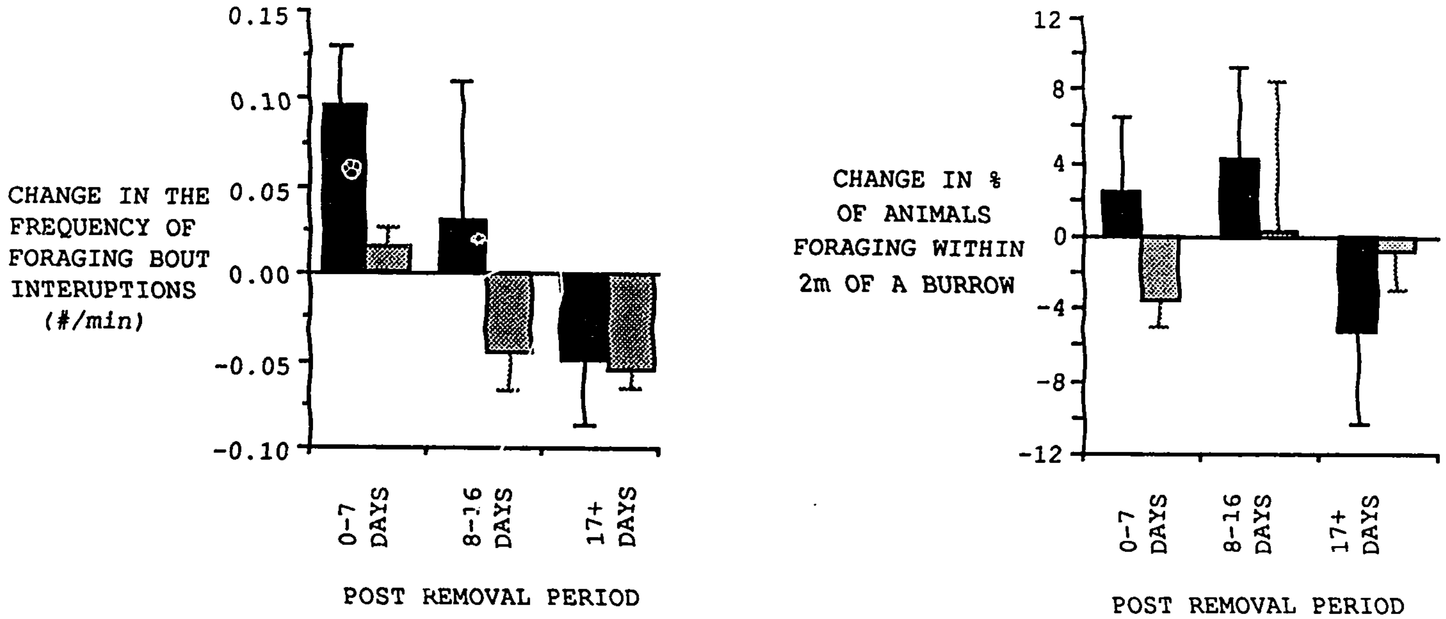


Figure 3.12 Mean (with SE bar) pre- to post- removal change in two factors for prairie dogs in 8 experimental (solid) and 8 control (stipple) groups during 3 post-removal periods. (* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$)

IV. GENERAL DISCUSSION

The purpose of this study was to gain further understanding of how the risk of predation affects the foraging behaviour of prairie dogs. The hypotheses I have addressed are based on the supposition that the foraging behaviour of prairie dogs has evolved within the context of a fitness tradeoff between safety and efficiency. For a given risk of predation and a given energetic demand there should exist an optimal foraging strategy that provides an individual with the greatest amount of energy with the least exposure to risk. My hypotheses further presume that prairie dogs assess, and are responsive to, risk of predation when foraging.

In chapter two I examine the relationship between the alertness of foraging prairie dogs and several factors that likely affect risk of predation. Alertness was highly variable among observations and correlated poorly with risk variables (all r's were <0.35). However, trends among the correlation coefficients of 6 different groups suggested that alertness was associated with several factors. As predicted, prairie dogs tended to forage more alertly when wind velocity was greater, when temperature was cooler, when the forager was nearer to the edge of the colony and farther from burrows, and when nearby (<40m) individuals were few. Of 9 measures of group size that enumerated pups, adults, or all prairie dogs within three different distance classes from a foraging individual, the number of adults within 20m of the focal individual was most strongly related to alertness. This relationship weakened with increasing distance from the forager and was non-existent for measures of group size that enumerated pups only. These results suggest that prairie dogs may be responsive to the presumed risk factors when foraging; however, they are not conclusive because the approach was correlative. These exploratory analyses have, however, identified several factors that potentially influence foraging behaviour and warrant further study. More specifically, my results suggest that adults, nearby adults in particular, are important to foraging prairie dogs, thus laying the ground work for future investigations of the proximate cues used by foraging prairie dogs to assess group size.

In chapter three I investigated experimentally the relationship between group size (one of the factors addressed in chapter 2) and the foraging behaviour of prairie dogs. I found that prairie dogs foraged more conservatively (more alertly and in less risky places) when in small vs large groups. Pups did not appear to influence a forager's assessment of group size (a result that corroborates the correlative analysis). The effect of group size reductions on the foraging behaviour of prairie dogs was both reversible and persisted for at least three weeks after manipulations. I conclude that group size and foraging behaviour are causally related and suggest that risk of predation is the most probable mechanism by which group size acts to influence foraging behaviour: my results are explicable if group size is a determinant of risk of predation and if prairie dogs are responsive to risk when foraging. Furthermore, assuming that prairie dogs forage less efficiently when foraging more conservatively, I conclude that enhanced foraging efficiency is a benefit of group living in black-tailed prairie dogs.

Having investigated the relationship between alertness and group size with both correlative and experimental approaches, I can compare the results of each and comment on their respective strengths and weaknesses. Among-observation variation weakened correlations between alertness and group size and my ability to detect an effect of group size manipulations. Variation confounded the correlative investigation to a greater degree than the experiment. The alertness of foraging prairie dogs was affected by manipulations of group size that removed all other individuals beyond approximately 40m of the focal animal; however, alertness was not associated with correlative measures of group size that considered individuals at a similar distance (colony adults, colony pups, and total colony). That the correlative analysis indicated that alertness was most strongly associated with the number of near adults suggests that the effect of group size manipulations would have been even greater had I removed near as well as distant neighbours.

Overall, the experimental approach better isolated the variable of interest from confounding factors and, in a "noisy" system such as this one, was the more powerful of the two approaches. Furthermore, the experimental approach allowed me to study the system at its extremes - much of the correlative data fell in the mid range of most factors and hence did little to illuminate their effects on alertness. On the other hand, the experimental approach is disruptive and limited in scope. A correlative analysis can simultaneously address several factors without disrupting the natural context of the behaviour of interest. In the study of animal behaviour each methodology has an appropriate time and place - the correlational approach is best used initially in an exploratory manner to identify potential relationships and to form hypotheses that can later be critically evaluated via experimentation.

APPENDIX A: DETERMINING AN OPTIMAL FOCAL LENGTH

In many studies behaviour is quantified by collecting data in a series of observation bouts of a fixed duration. When choosing a suitable duration, a researcher must consider many factors: the question(s) being asked, the study species, the behaviour(s) of interest, and the endurance limitations of the observer. Despite its potential to have cascading effect throughout the entire study, the choice of an appropriate bout duration has received little attention from behaviourists. In fact it is not even mentioned in otherwise excellent introductory texts on behavioral methods (eg. Martin and Bateson 1986) and is rarely considered in published papers. Here I discuss an objective approach to determining a statistically optimal bout duration. The method requires a sample of behavioral observations that are each as long as the longest observation duration the researcher deems to be practical. I apply the method to data collected from black-tailed prairie dogs.

Bout length can affect the **resolving power** of collected data (the likelihood of detecting statistically-significant differences between groups or relationships among measured factors). The standard error (SE) of a sample is a statistical measure of its resolving power; the smaller the standard error the greater the resolving power of the data. Here I define a statistically optimal bout duration as one that minimises the SE of a sample of data that can be collected in a fixed period of time. Thus, from a range of practical alternatives one can select an optimal focal duration by determining that which minimizes the SE of the sample.

Bout duration influences the two determinants of SE - both the size of the sample (n) and its variance (s^2). As bout length increases, fewer observations can be collected in a given period of time; however, the variance among observations decreases because each observation is a more representative sample of behaviour. An extremely long or short observation duration would likely not minimize SE because it would generate either few or highly variable observations: some intermediate observation length should be optimal. Another consideration that enters into the determination of an optimal focal duration is the length of the between-observation interval. To make the most of available research time, an observer would ideally make the transition from one observation to the next with a negligible loss of time; however, time may be taken between observations to locate the next focal animal, to record notes specific to the observation just completed, or to collect or record other data. Obviously, a long inter-focal interval reduces the number of observations that can be collected in a given period of time.

The SE associated with a given focal length is calculated as follows:

$$\text{duration-specific SE} = \sqrt{\frac{\text{duration-specific } s^2}{T_f/(L_b + I)}}$$

Where s^2 = duration specific sample variance, T_f = total fixed observation time, L_b = length of an observation bout, and I = average inter-focal duration.

During the summer of 1989 I collected a sample of 59, ten-minute-long, focal animal (Altmann 1974) observations of prairie dog foraging behaviour from which I determined the percentage of each that was devoted to feeding and computed the sample variance (s^2) for this measure of behaviour. I then subdivided each observation into 5-, 2-, 1-, and 0.5 minute-long segments and for this same measure of behaviour calculated s^2 for each segment length (Appendix A - Fig. 1). Using the above formula, for inter-focal intervals of 0, 1, 3, 5, and 7 minutes, I computed SE's for observation durations ranging from 0.25 - 10 minutes. The resulting family of SE vs focal duration curves are plotted in Appendix A - Fig. 2.

Each curve of the family exhibits the same general shape: as the observation duration approaches 0, SE is stable or decreases gradually. Near 0, at a critical point, the function increases sharply and eventually becomes asymptotic to the y-axis.

Not surprisingly the shorter the length of the inter-focal interval, the greater the resolving power of the collected sample. Furthermore, with shorter inter-focal periods (0 and 1 minutes) there is a salient optimal focal duration of between 30 and 60 seconds. On the other hand, for longer inter-focal periods, above a lower threshold (beneath which resolving power becomes greatly diminished) no focal duration is markedly optimal (Appendix A - Fig. 2).

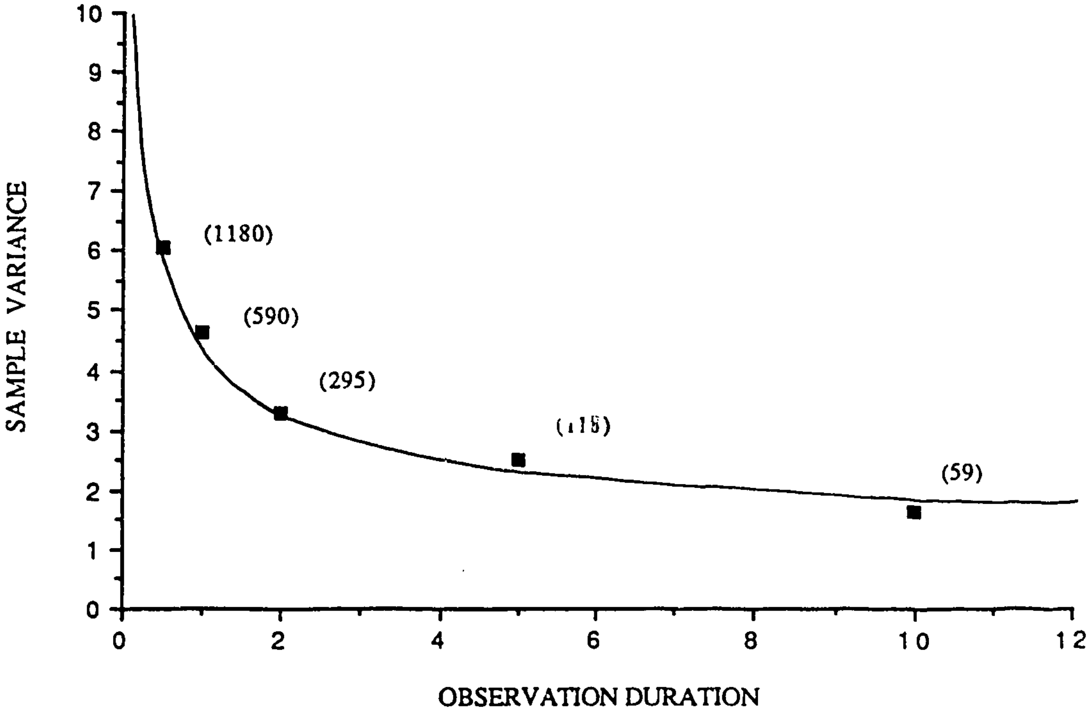
The inter-focal interval of observations collected for this thesis was between 4 and 5 minutes. Given this, considering only one measure of behaviour (the % time devoted to feeding) an observation duration of between 2 and 3 minutes should maximise the resolving power of collected data. During the summer of 1989 I used an arbitrarily determined observation duration of 5 minutes; however, after completing this focal length analyses I switched to a focal length of 3 minutes for collecting observations during the summer of 1990.

LITERATURE CITED

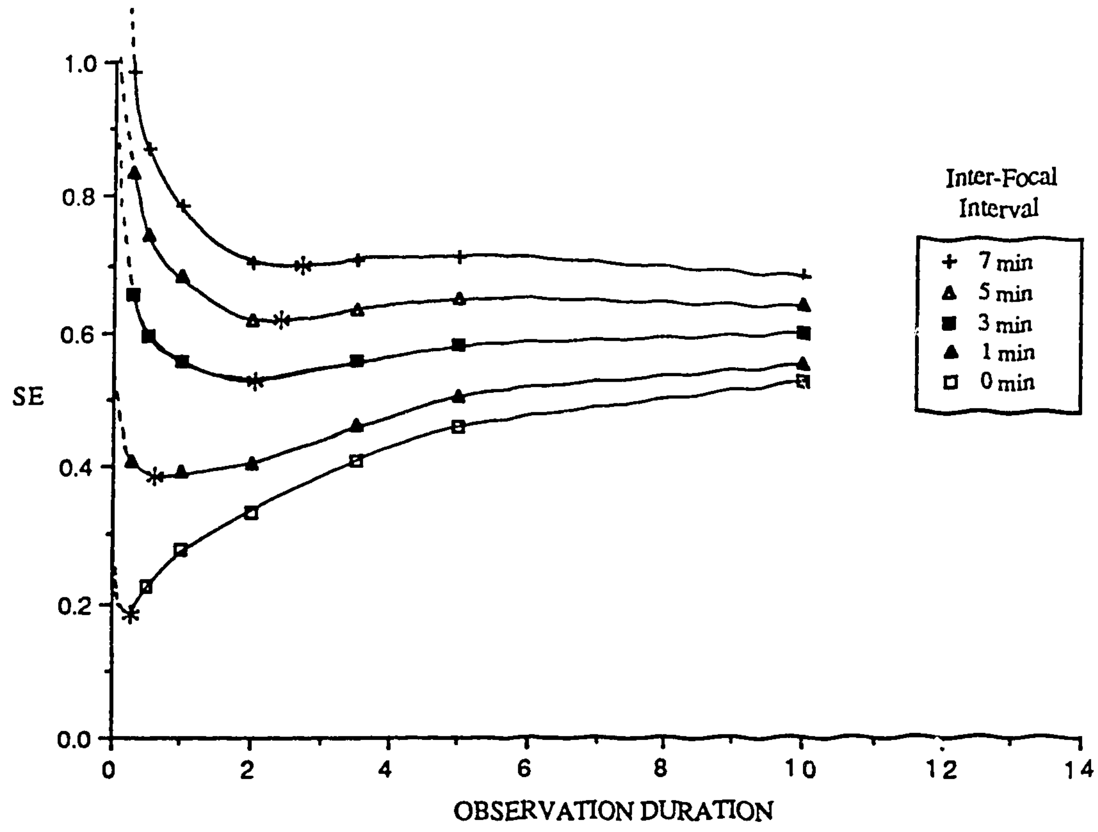
Altmann, J. 1974. Observational study of behaviour: Sampling methods. Behaviour. 49:227-267.

Martin, P., and P. Bateson. 1986. Measuring Behaviour. Cambridge, Cambridge.

Appendix A - Figure 1. Sample variance as a function of observation duration. (Sample size is indicated parenthetically.)



Appendix A - Figure _. Standard error as a function of focal length for 4 different inter-focal intervals. (* = The optimal focal length for each inter-focal interval.)



APPENDIX B: BEHAVIORAL RESPONSES OF INDIVIDUAL CONTROL AND EXPERIMENTAL GROUPS TO REMOVAL, REPLACEMENT, AND PERMANENT REMOVAL MANIPULATIONS.

The following 12 tables present the raw, group-by-group data used to calculate means and standard errors that are graphically presented in Figs. 3.1 - 3.13. Tables 1-11 correspond to Figs. 3.1 - 3.11, while data in Table 12 is found in Figs. 3.12 and 3.13.

	FEEDING			HEADBOB			UPRIGHT			ALERT		
Group	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp	Cont.	Diff.
1	-11.2	-6.5	-4.7	0.1	-1.4	1.5	9.6	8.2	1.5	1.5	-0.2	1.8
2	-21.3	1.9	-23.2	7.6	1.6	6.0	6.6	-0.2	6.8	7.1	-3.3	10.4
3	-7.5	-2.0	-5.6	4.6	-1.8	6.4	3.2	4.1	-0.1	-0.3	-0.4	0.1
4	-4.3	-3.9	-0.5	2.7	-0.8	3.4	1.1	6.8	-5.8	0.7	-2.2	2.8
5	-9.1	-0.8	-8.3	3.6	-2.2	5.8	3.7	2.8	0.9	1.9	0.2	1.6
6	-15.1	-9.5	-5.6	2.5	0.8	1.6	12.9	10.6	2.4	-0.3	-1.9	1.6
7	-5.8	2.5	-8.3	-1.1	1.6	-2.6	4.7	-3.1	7.8	2.1	-0.8	3.0
8	-8.5	1.1	-9.4	8.6	-0.9	9.6	-1.7	-1.1	-0.6	1.4	0.9	0.5
A	-13.3	1.5	-14.8	0.8	1.6	-0.8	7.5	-2.8	10.4	5.0	-0.2	5.3
B	-10.2	1.5	-11.8	9.1	-1.7	10.7	1.1	1.9	-0.8	0.1	-1.7	1.8
C	-2.7	2.8	-5.5	3.1	0.1	2.9	-1.7	-1.7	-0.1	1.3	-1.3	2.6
D	-17.0	5.4	-22.4	3.1	1.9	4.9	10.7	-3.3	14.0	3.3	-0.3	3.5
mean	-10.5	-0.5	-10.0	3.7	-0.4	4.1	4.8	1.9	3.0	2.0	-0.9	2.9

Appendix B - Table 1. Pre- to post-removal change of the percent of total foraging time (%) that prairie dogs in 12 experimental (Exp.) and 12 control (Cont.) groups devoted to Feeding, Headbob, Upright, and Alert postures. The difference (Diff.) in the response of paired control and experimental groups (Exp.- Cont.) is also shown. Groups 1-8 were part of temporary manipulations, while group pairs A-D were part of permanent manipulations.

	FEEDING			HEADBOB			UPRIGHT			ALERT		
Group	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp	Cont.	Diff.
1	0.95	0.28	0.66	0.47	-0.83	1.30	0.42	1.15	-0.72	0.40	-0.03	0.43
2	5.41	0.04	5.37	3.76	0.04	3.72	1.14	0.07	1.08	1.26	-0.26	1.52
3	0.81	-0.78	1.59	1.26	-0.87	2.13	-0.06	0.16	-0.23	0.10	-0.11	0.21
4	0.84	-0.72	1.56	0.77	-0.84	1.61	0.15	0.27	-0.12	0.04	-0.30	0.34
5	1.27	-0.21	1.48	0.76	-0.48	1.24	0.49	0.35	0.14	0.27	0.16	0.11
6	2.24	0.14	2.09	0.49	-0.42	0.91	2.15	1.04	1.11	0.02	-0.09	0.11
7	-0.34	-0.68	0.34	-0.65	-0.02	-0.63	0.43	-0.50	0.92	0.35	-0.21	0.55
8	2.90	-1.56	4.46	3.29	-0.05	3.34	0.12	-1.33	1.45	0.32	0.06	0.26
A	0.52	-1.77	2.29	0.18	-1.34	1.51	0.57	-0.34	0.90	0.44	-0.14	0.57
B	2.57	-0.99	3.56	2.45	-0.95	3.40	0.26	-0.48	0.74	0.16	-0.12	0.28
C	2.27	-0.42	2.69	2.54	-0.39	2.92	-0.12	-0.21	0.10	0.30	-0.02	0.32
D	2.27	-0.79	3.05	1.95	-0.19	2.14	0.95	-0.80	1.74	0.34	-0.03	0.37
mean	1.81	-0.62	2.43	1.44	-0.51	1.97	0.54	-0.05	0.59	0.33	-0.09	0.42

Appendix B - Table 2. Pre- to post-removal change in the frequency of occurrence (#/minute) of bouts of Feeding, Headbob, Upright, and Alert postures for prairie dogs in 12 experimental (Exp.) and 12 control (Cont.) groups. The difference (Diff.) in the response of paired control and experimental groups (Exp.- Cont.) is also shown. Groups 1-8 were part of temporary manipulations, while group pairs A-D were part of permanent manipulations.

	FEEDING			HEADBOB			UPRIGHT			ALERT		
Group	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp	Cont.	Diff.
1	-3.00	-1.30	-1.70	-0.39	0.39	-0.78	1.58	-0.49	2.07	0.61	0.26	0.35
2	-7.11	0.59	-7.70	-0.08	0.41	-0.49	-0.18	-0.25	0.08	-0.39	-2.35	1.96
3	-1.24	1.21	-2.44	0.25	0.05	0.20	0.89	1.32	-0.42	-0.21	0.01	-0.22
4	-0.39	0.36	-0.75	0.10	0.29	-0.19	-0.28	1.14	-1.42	1.60	-1.51	3.10
5	-2.30	0.38	-2.68	0.17	-0.12	0.29	2.41	0.43	1.98	1.53	-0.73	2.26
6	-5.36	-0.70	-4.66	0.08	0.35	-0.28	-0.05	-1.06	1.01	-0.03	-0.71	0.68
7	-2.00	1.38	-3.38	-0.44	0.18	-0.61	1.09	-0.28	1.37	-0.27	-1.01	0.74
8	-4.02	1.13	-5.16	-0.37	-0.27	-0.11	-1.44	0.85	-2.29	-0.26	-0.40	0.14
A	-2.14	0.27	-2.42	0.04	0.63	-0.58	2.46	-1.70	4.16	1.16	-0.56	1.73
B	-3.76	1.24	-5.00	0.50	0.27	0.23	-0.71	1.57	-2.28	-0.51	0.08	-0.59
C	-4.06	5.36	-9.42	-0.18	0.25	-0.43	-0.26	-0.16	-0.10	0.83	-0.66	1.59
D	-6.58	2.71	-9.29	-0.49	-0.19	-0.30	2.96	0.93	2.02	-1.30	-0.20	-1.09
mean	-3.50	1.05	-4.55	-0.07	0.19	-0.25	0.71	0.19	0.51	0.23	-0.65	0.88

Appendix B - Table 3. Pre- to post-removal change in the average duration (seconds) of bouts of Feeding, Headbob, Upright, and Alert postures for prairie dogs in 12 experimental (Exp.) and 12 control (Cont.) groups. The difference (Diff.) in the response of paired control and experimental groups (Exp.- Cont.) is also shown. Groups 1-8 were part of temporary manipulations, while group pairs A-D were part of permanent manipulations.

	Frequency of Foraging Period Interuptions (#/minute)			Percentage of Foragers Within 2m of a Burrow (%)			Distance From Edge of Colony (m)			Height of Vegetation Foraged in (category units)		
Group	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.
1	0.11	-0.06	0.17	-.004	-0.13	0.13	4.68	-3.68	8.36	-0.38	-0.16	-0.22
2	0.34	-0.11	0.45	0.20	-0.12	0.32	-2.90	-5.30	2.39	-0.04	0.11	-0.15
3	0.08	0.01	0.07	-0.01	0.00	-0.02	3.99	1.03	2.96	-0.15	-0.08	-0.07
4	0.12	-0.05	0.18	0.08	-0.01	0.09	4.03	-4.87	8.91	-0.05	0.13	-0.18
5	0.14	0.03	0.12	-0.03	-0.07	0.04	2.82	-2.17	4.99	0.04	0.05	-0.01
6	0.13	-0.12	0.26	0.00	0.05	-0.05	-1.82	10.25	-12.07	0.30	0.00	0.30
7	0.20	-0.07	0.27	0.15	0.08	0.07	-2.78	4.10	-6.88	-0.33	-0.06	-0.27
8	0.05	-0.07	0.12	0.12	0.00	0.12	-1.30	-3.10	1.80	-0.05	-0.14	0.09
A	0.18	0.16	0.02	0.13	0.00	0.13	5.53	-8.78	14.31	-0.08	0.13	-0.21
B	0.07	0.03	0.04	-0.07	0.08	-0.15	0.21	1.22	-1.01	-0.19	-0.08	-0.11
C	0.21	0.03	0.18	0.04	-0.08	0.13	6.37	-2.27	8.64	-0.21	-0.01	-0.20
D	0.14	-0.02	0.16	-0.18	-0.06	-0.13	5.29	-0.49	5.78	0.09	0.02	0.07
mean	0.15	-0.02	0.17	0.04	-0.02	0.06	2.01	-1.17	3.18	-0.09	-0.01	-0.08

Appendix B - Table 4. Pre- to post-removal change of four measured factors for prairie dogs in 12 experimental (Exp.) and 12 control (Cont.) groups. The difference (Diff.) in the response of paired control and experimental groups (Exp.- Cont.) is also shown. Group pairs 1-8 were part of temporary manipulations, while group pairs A-D were part of permanent manipulations.

Group	FEEDING Exp.	FEEDING Cont.	FEEDING Diff.	HEADBOB Exp.	HEADBOB Cont.	HEADBOB Diff.	UPRIGHT Exp.	UPRIGHT Cont.	UPRIGHT Diff.	ALERT Exp	ALERT Cont.	ALERT Diff.
1	17.9	0.0	17.9	-0.7	-0.7	0.0	-15.2	-0.4	-14.9	-1.9	1.1	-3.0
2	19.9	-3.2	23.0	-9.9	-0.5	-9.3	-2.2	2.7	-5.0	-7.7	1.0	-8.7
3	5.3	-4.1	9.3	-0.5	-0.9	0.4	-3.9	4.6	-8.5	-0.9	0.4	-1.3
4	-5.2	-3.8	-1.4	-2.3	-0.4	-1.8	9.7	4.4	5.3	-2.2	-0.1	-2.1
5	5.1	0.9	4.2	-5.1	0.7	-5.8	1.2	-1.3	2.5	-1.2	-0.3	-0.9
6	2.3	10.9	-8.6	-4.7	0.2	-5.0	1.6	-12.8	14.4	0.8	1.7	-0.9
7	-0.4	-2.2	1.9	4.6	-1.5	6.1	-3.3	3.1	-6.4	-0.9	0.6	-1.5
8	-0.2	-0.8	0.6	-4.3	-0.4	-3.9	7.4	3.5	3.9	-2.9	-2.3	-0.6
mean	5.6	-0.3	5.9	-2.9	-0.5	-2.4	-0.6	0.5	-1.1	-2.1	0.3	-2.4

Appendix B - Table 5. Pre- to post-replacement change of the percent of total foraging time (%) that prairie dogs in 8 experimental (Exp.) and 8 control (Cont.) groups devoted to Feeding, Headbob, Upright, and Alert postures. The difference (Diff.) in the response of paired control and experimental groups (Exp.- Cont.) is also shown. All 8 group pairs were part of temporary manipulations.

	FEEDING			HEADBOB			UPRIGHT			ALERT		
Group	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp	Cont.	Diff.
1	-1.62	-0.56	-1.06	-0.52	-0.12	-0.41	-1.20	-0.38	-0.83	-0.37	0.07	-0.44
2	-5.35	-0.19	-5.16	-4.42	-0.15	-4.27	-0.45	0.00	-0.45	-1.42	0.11	-1.53
3	-0.46	-0.29	-0.18	-0.74	-0.83	0.09	0.06	0.65	-0.59	-0.13	-0.02	-0.12
4	-0.51	-0.60	0.09	-0.94	-0.47	-0.46	0.49	0.01	0.48	-0.14	0.00	-0.14
5	-2.36	-0.94	-1.42	-2.61	-0.70	-1.91	0.37	-0.18	0.55	-0.17	-0.23	0.07
6	0.13	-0.79	0.92	-1.47	-0.21	-1.25	1.66	-1.16	2.83	0.23	0.11	0.12
7	-0.15	-0.43	0.29	0.41	-1.06	1.47	-0.45	0.43	-0.88	-0.21	0.07	-0.28
8	-2.15	1.49	-3.64	-2.11	-0.52	-1.59	0.46	1.72	-1.26	-0.20	-0.41	0.21
mean	-1.56	-0.29	-1.27	-1.55	-0.51	-1.04	0.12	0.14	-0.02	-0.30	-0.04	-0.26

Appendix B - Table 6. Pre- to post-replacement change of the frequency of occurrence (#/minute) of bouts of Feeding, Headbob, Upright Alert postures for prairie dogs in 8 experimental (Exp.) and 8 control (Cont.) groups. The difference (Diff.) in the response of paired control and experimental groups (Exp.- Cont.) is also shown. All 8 group pairs were part of temporary manipulations.

	FEEDING			HEADBOB			UPRIGHT			ALERT		
Group	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp	Cont.	Diff.
1	6.48	-0.29	6.77	0.38	-0.40	0.78	-1.25	0.55	-1.80	-1.00	0.96	-1.96
2	5.37	-0.38	5.75	-0.13	-0.21	0.08	0.06	1.54	-1.48	0.15	0.15	0.00
3	2.09	0.31	1.77	0.12	0.35	-0.23	-1.23	-0.64	-0.59	-1.28	0.21	-1.49
4	-0.72	0.20	-0.92	0.12	-0.08	0.20	1.30	1.23	0.08	-2.67	-0.22	-2.45
5	4.30	0.10	4.20	0.02	0.22	-0.20	-2.21	0.47	-2.68	-0.82	0.94	-1.76
6	0.81	2.15	-1.33	-0.20	0.10	-0.30	-1.00	-0.06	-0.93	-0.14	1.24	-1.38
7	0.70	1.73	-1.03	0.66	0.11	0.55	-0.20	0.15	-0.35	-0.07	1.10	-1.17
8	1.80	0.48	1.32	0.37	0.11	0.26	1.35	-0.54	1.89	-1.10	-0.37	-0.73
mean	2.61	0.54	2.07	0.17	0.02	0.14	-0.40	0.34	-0.73	-0.87	0.50	-1.37

Appendix B - Table 7. Pre- to post-replacement change of the average duration (seconds) of bouts of Feeding, Headbob, Upright, and Alert postures for prairie dogs in 8 experimental (Exp.) and 8 control (Cont.) groups. The difference (Diff.) in the response of paired control and experimental groups (Exp.- Cont.) is also shown. All 8 group pairs were part of temporary manipulations.

Group	Frequency of Foraging Period Interuptions (#/minute)			Percentage of Foragers Within 2m of a Burrow (%)			Distance From Edge of Colony (m)			Height of Vegetation Foraged in (category units)		
	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.
1	-0.06	0.04	-0.10	0.04	0.16	-0.12	3.14	-3.38	6.52	-0.01	0.23	-0.24
2	-0.25	-0.02	-0.23	-0.24	0.02	-0.26	4.95	1.44	3.51	0.03	-0.07	0.09
3	0.03	-0.03	0.06	-0.05	0.02	-0.07	5.65	-9.75	15.39	-0.07	0.22	-0.29
4	-0.09	-0.01	-0.08	-0.17	-0.05	-0.13	-5.80	2.46	-8.26	0.00	0.02	-0.01
5	0.01	0.06	-0.05	0.04	-0.01	0.05	0.28	5.67	-5.38	0.17	0.07	0.10
6	-0.06	0.19	-0.25	0.00	-0.08	0.08	-0.55	-2.23	1.68	0.21	0.00	0.21
7	-0.33	0.10	-0.43	0.05	0.01	0.04	-6.30	0.47	-6.77	0.18	-0.24	0.42
8	-0.20	-0.04	-0.16	-0.07	0.02	-0.08	-0.33	3.32	-3.65	0.07	0.01	0.06
mean	-0.12	0.04	-0.16	-0.05	0.01	-0.06	0.13	-0.25	0.38	0.07	0.03	0.04

Appendix B - Table 8. Pre- to post-removal change of four measured factors for prairie dogs in 8 experimental (Exp.) and 8 control (Cont.) groups. The difference (Diff.) in the response of paired control and experimental groups (Exp.- Cont.) is also shown. All 8 group pairs were part of temporary manipulations.

Period	Group	FEEDING Exp.	FEEDING Cont.	FEEDING Diff.	HEADBOB Exp.	HEADBOB Cont.	HEADBOB Diff.	UPRIGHT Exp.	UPRIGHT Cont.	UPRIGHT Diff.	ALERT Exp	ALERT Cont.	ALERT Diff.
	A	-9.2	3.3	-12.5	-0.8	-1.0	0.1	5.6	-1.4	7.1	4.4	-0.9	5.4
0-7	B	-10.3	-6.0	-4.3	9.9	2.2	7.6	0.3	2.8	-2.5	0.1	0.9	-0.8
Days	C	-1.5	7.0	-8.5	2.7	-1.7	4.5	-2.4	-3.6	1.1	1.2	-1.7	2.9
	D	-19.2	2.0	-21.2	5.8	0.0	5.8	11.8	-2.5	14.3	1.5	0.5	1.1
	mean	-10.0	1.6	-11.6	4.4	-0.1	4.5	3.8	-1.2	5.0	1.8	-0.3	2.1
	A	-16.5	-9.6	-6.9	6.7	-0.5	7.2	10.2	10.2	0.1	-0.4	0.0	-0.4
8-16	B	-17.8	-22.0	4.2	1.9	0.7	1.1	14.1	21.3	-7.1	1.8	0.0	1.8
Days	C	-10.5	7.1	-17.7	4.6	2.6	2.0	5.6	-7.5	13.2	0.3	-2.2	2.5
	D	-31.3	2.2	-29.1	19.6	0.3	19.3	11.8	1.9	9.9	-0.1	0.0	-0.1
	mean	-19.0	-6.7	-12.4	8.2	0.7	7.4	10.5	6.5	5.7	0.4	-0.6	0.9
	A	-30.6	-11.4	-19.2	16.6	-0.6	17.3	12.2	13.1	-1.0	1.8	-1.0	2.9
17 +	B	-15.4	-11.7	-3.8	-1.0	5.5	-6.5	17.2	6.6	10.6	-0.8	-0.4	-0.3
Days	C	-7.2	-6.8	-0.4	1.9	5.9	-4.1	5.0	2.6	2.4	0.3	-1.7	2.0
	D	-35.4	-1.3	-34.2	23.0	1.1	21.9	10.9	0.2	10.6	1.6	-0.1	1.7
	mean	-22.2	-7.8	-14.4	10.1	3.0	7.1	11.3	5.6	5.7	0.7	-0.8	1.6

Appendix B - Table 9. Pre- to post-removal change of the percent of total foraging time (%) that prairie dogs in 4 experimental (Exp.) and control (Cont.) groups devote to Feeding, Headbob, Upright, and Alert postures. Data for three post-removal periods are presented (0-7 days, 8-16 days, and 17 + days). The difference (Diff.) in the response of paired control and experimental groups (Exp.- Cont.) is also shown. All 4 group pairs were part of permanent manipulations.

Period	Group	FEEDING Exp.	FEEDING Cont.	FEEDING Diff.	HEADBOB Exp.	HEADBOB Cont.	HEADBOB Diff.	UPRIGHT Exp.	UPRIGHT Cont.	UPRIGHT Diff.	ALERT Exp	ALERT Cont.	ALERT Diff.
	A	-0.48	-1.19	0.71	-0.60	-0.70	0.11	0.25	-0.44	0.70	0.30	-0.17	0.47
1-7	B	2.74	-1.67	4.41	2.82	-1.17	3.99	0.10	-0.51	0.60	0.17	0.02	
Days	C	1.50	-1.48	1.98	1.75	-0.59	2.34	-0.18	-0.21	0.02	0.27	-0.07	0.33
	D	2.45	-0.60	3.06	2.16	0.10	2.05	0.90	-0.77	1.67	0.16	0.07	0.09
	mean	1.55	-0.99	2.54	1.53	-0.59	2.12	0.27	-0.48	0.75	[illegible]	-0.04	0.26
	A	0.36	-0.24	0.60	0.66	-0.91	1.57	0.53	0.88	-0.35	-0.08	-0.01	-0.06
8-16	B	0.07	-1.37	1.44	-0.55	-0.94	0.39	1.01	[illegible]	-0.38	0.25	0.01	0.24
Days	C	1.47	-1.11	2.58	1.12	-0.63	1.75	0.51	1.39	1.20	0.16	-0.11	0.26
	D	3.03	0.21	2.82	3.47	0.26	3.20	0.77	-0.70	[illegible]	0.15	0.06	0.09
	mean	1.23	-0.63	1.86	1.17	-0.56	1.73	0.70	0.38	0.32	0.12	0.01	0.13
	A	1.14	0.43	0.71	1.69	-0.85	2.55	0.79	1.53	-0.74	0.17	-0.14	0.32
17 +	B	1.67	0.60	1.07	-0.59	0.55	-1.14	2.71	0.99	1.72	-0.16	0.02	-0.18
Days	C	1.42	0.18	1.24	1.18	0.41	0.78	0.47	-0.03	0.49	0.08	-0.07	0.14
	D	2.65	-0.74	3.38	3.08	-0.13	3.21	0.83	-0.70	1.53	0.23	-0.02	0.25
	mean	1.72	0.12	1.60	1.34	-0.7	1.35	1.20	0.45	0.75	0.08	-0.05	0.13

Appendix B - Table 10. Pre- to post-removal change of the frequency of occurrence (#/minute) of bouts of Feeding, Headbob, Upright, and alert postures for prairie dogs in 4 experimental (Exp.) and 4 control (Cont.) groups. Data for three post-removal periods are presented (0-7 days, 8-16 days, and 17 + days). The difference (Diff.) in the response of paired control and experimental groups (Exp.- Cont.) is also shown. All 4 group pairs were art of permanent manipulations.

Period	Group	FEEDING			HEADBOB			UPRIGHT			ALERT		
		Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp	Cont.	Diff.
1-7 Days	A	-0.30	1.74	-2.05	-0.24	0.15	-0.40	2.81	-0.58	3.39	2.04	-0.95	3.00
	B	-4.02	0.79	-4.82	0.50	0.84	-0.33	-1.00	1.95	-2.95	-0.35	2.03	-2.38
	C	-3.17	5.61	-8.78	-0.09	0.09	-0.18	-0.37	-0.94	0.57	0.78	-0.86	1.64
	D	-7.14	1.49	-8.63	-0.29	0.05	-0.25	-3.55	1.28	2.27	-1.17	0.16	-1.34
	mean	-3.66	2.41	-6.07	-0.01	0.29	-0.29	1.25	0.43	0.82	0.32	0.10	0.23
8-16 Days	A	-1.84	-1.02	-0.81	0.80	0.20	0.60	2.41	0.96	1.46	-7.64	-0.29	0.90
	B	-2.60	0.02	-2.62	0.74	0.81	-0.08	2.05	2.43	-0.38	1.99	1.68	-1.51
	C	-3.63	0.85	4.48	0.31	0.94	-0.63	1.27	-0.35	2.12	10.23	-1.09	1.16
	D	-9.16	-1.77	-7.39	0.84	0.15	0.69	4.06	0.94	3.13	0.84	-0.16	-0.74
	mean	-4.73	-0.48	-3.83	0.67	0.53	0.14	2.44	0.87	1.58	-0.01	0.04	-0.05
17 + Days	A	-3.54	-1.94	-1.61	1.26	0.24	1.02	2.62	0.41	2.21	1.54	-1.17	2.71
	B	-3.86	-0.80	-3.06	0.02	0.36	-0.34	1.15	0.28	0.86	-0.93	-0.72	-0.21
	C	-3.35	-3.04	-0.30	-0.07	0.45	-0.51	1.35	0.36	0.99	-0.04	-0.93	0.89
	D	-9.64	0.71	-10.35	1.46	0.30	1.16	3.41	1.60	1.80	-0.64	0.12	-0.76
	mean	-5.10	-1.27	-3.83	0.67	0.34	0.33	[illegible]	0.66	1.47	-0.02	-0.68	0.66

Appendix B - Table 11. Pre- to post-removal change of the average duration (seconds) of bouts of Feeding, Headbob, Upright, and alert postures for prairie dogs in 4 experimental (Exp.), and 4 control (Cont.) groups. Data for three post-removal periods are presented (0-7 days, 8-16 days, and 17 + days). The difference (Diff.) in the response of paired control and experimental groups (Exp.- Cont.) is also shown. All 4 group pairs were part of permanent manipulations.

Period	Group	Frequency of Foraging Period Interruptions (#/minute)			Percentage of Foragers Within 2m of a Burrow (%)			Distance From Edge of Colony (m)			Height of Vegetation Foraged in (category units)		
		Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp.	Cont.	Diff.	Exp	Cont.	Diff.
	A	0.18	0.01	0.17	12.1	-4.3	16.4	-5.28	-6.21	0.93	-0.02	-0.04	0.02
1-7	B	0.03	0.04	-0.02	-1.1	0.3	-1.4	-1.05	-2.32	1.28	-0.58	-0.34	-0.24
Days	C	0.07	0.01	0.05	5.2	-6.5	11.7	6.99	-1.72	8.71	-0.22	-0.04	-0.18
	D	0.09	0.00	0.09	-6.3	-3.7	-2.6	2.98	-0.41	3.39	0.12	-0.02	-0.14
	mean	0.09	0.02	0.06	2.5	-3.6	6.0	0.91	-2.67	3.58	0.18	-0.11	-0.06
	A	-0.14	-0.06	-0.08	-2.6	-4.3	1.8	-7.64	-2.07	-5.57	0.06	0.14	-0.08
8-16	B	0.16	-0.01	-0.17	-5.3	-12.2	6.9	1.99	-6.35	8.34	-0.13	-0.06	-0.07
Days	C	0.18	-0.05	0.22	9.0	24.3	-15.3	10.23	1.22	9.01	-0.26	-0.07	-0.19
	D	-0.06	-0.10	0.05	16.0	-6.3	22.4	0.84	-1.70	2.55	0.34	-0.09	0.43
	mean	0.03	-0.05	0.09	4.3	0.4	3.9	1.36	-2.22	3.58	0.00	-0.02	0.02
	A	-0.13	-0.05	-0.8	9.0	-2.8	11.9	-4.13	-7.35	3.22	0.00	0.52	-0.52
17 +	B	-0.03	-0.07	0.04	-5.3	-0.5	-4.8	9.80	0.60	9.20	0.24	-0.21	0.44
Days	C	-0.11	-0.04	-0.07	-8.1	5.0	-13.1	9.99	-6.14	16.14	-0.25	-0.07	-0.18
	D	0.03	-0.09	0.13	-16.2	-4.7	-11.5	0.53	-3.36	3.89	0.57	-0.02	0.60
	mean	-0.06	-0.06	0.01	-5.1	-0.7	-4.4	4.05	-4.06	8.12	0.14	0.05	0.08

Appendix B - Table 12. Pre-post removal change of four measured factors for prairie dogs in 4 experimental (Exp.) and 4 control (Cont.) groups. Data for three post-removal periods are presented (0-7 days, 8-16 days, and 17 + days). The difference (Diff.) in the response of paired control and experimental groups (Exp.- Cont.) is also shown. All 4 group pairs were part of permanent manipulations.

APPENDIX C: PRE- AND POST-REMOVAL COMPOSITION OF EXPERIMENTAL GROUPS

Appendix C - Table 1. Pre-removal attributes of 12 experimental groups.

Group	Area (ha)		Number		Density (#/ha)		
	Group	Focal Cot.	Adults	Pups	Adults	Pups	Mounds[1]
1	0.98	0.46	10	16	10	16	133
2	0.82	0.27	15	18	18	22	148
3	1.43	0.20	12	19	8	13	225
4	0.89	0.36	16	18	18	20	142
5	1.50	0.23	48	47	32	32	204
6	1.40	0.15	42	90	30	64	-
7	1.20	0.19	41	76	34	63	232
8	1.40	0.44	24	96	34	63	232
A	1.75	0.38	48	112	27	64	163
B	3.50	0.32	58	123	17	35	-
C	1.00	0.13	19	64	19	64	254
D	0.74	0.37	22	48	29	65	200

[1] Mound density calculated for the focal coterie only.

Appendix C - Table 2. Post-removal composition of 12 experimental groups.

Group	Age Class	REMOVED Focal Coterie	REMOVED Adjacent Coteries	REMOVED Non-adj. Coteries	REMAINING Focal Coterie	REMAINING Adjacent Coteries	REMAINING Non-adj. Coteries
1	adults	0	5	-	5	0	-
	pups	8	8	-	0	0	-
2	adults	0	6	4	5	0	0
	pups	8	2	7	1	0	0
3	adults	0	5	5	5	1	0
	pups	7	5	5	0	0	0
4	adults	0	3	2	3	2	2
	pups	8	10	0	0	1	0
5	adults	4[1]	16	16	5	8	2
	pups	0	23	8	9	5	2
6	adults	0	9	17	5	2	1
	pups	0	19	53	4	2	10
7	adults	0	11	16	6	4	2
	pups	0	28	34	11	2	2
8	adults	0	8	8	6	0	2
	pups	0	34	45	15	0	2
A	adults	0	11	28	3	3	3
	pups	0	18	85	6	0	3
B	adults	0	5	40	5	2	3
	pups	0	28	114	16	0	5
C	adults	0	6	8	4	1	0
	pups	11	20	23	2	0	8
D	adults	4	7	6	4	0	1
	pups	30	10	5	3	0	0

[1] I have included these adults in the "removed" column because they were not present in the focal coterie for the entire post-removal period.