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Recommended Citation

Verdolin, J. L., & Slobodchikoff, C. N. (2002). Vigilance and predation risk in Gunnison's prairie dogs (*Cynomys gunnisoni*). *Canadian Journal of Zoology*, 80(7), 1197-1203.

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Vigilance and Predation Risk in Gunnison's Prairie Dogs (*Cynomys gunnisoni*)

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ABSTRACT

Group living in animals is believed to confer advantages related to a decrease in predation risk and an energetic trade-off between vigilance and foraging efficiency. Eight Gunnison's prairie dog, Cynomys gunnisoni, colonies in Flagstaff, Arizona (elevation 2300 m), were studied from April to August 2000 to examine the adaptive significance of colonial living in the context of predation risk and antipredator behavioral strategies. Each colony was sampled once every 10 days for a period of 3 h. Upright and quadrepedal vigilance was recorded using scan samples. All predation events were recorded. Results suggest that vigilant behavior in Gunnison's prairie dogs is an antipredator strategy because the animals oriented more frequently towards the periphery of the colony while vigilant. Gunnison's prairie dogs engaged in posting, an upright bipedal posture, more frequently than scanning, a quadrepedal posture. Furthermore, there was no relationship between either form of vigilance and population size. The proportion of animals vigilant decreased significantly only on the two smallest colonies as colony size increased. On larger colonies there was no relationship between the proportion of animals vigilant and colony size. The lack of change in the proportion of animals vigilant in larger populations may be a function of perceived risk rather than actual individual risk.

Introduction

Several investigators have demonstrated a causal relationship between predation and the evolution of group living in animals (Hamilton 1971; Pulliam 1973). When animals live in groups, the likelihood of detecting a predator may increase (Hoogland 1981; Clutton-Brock et al. 1999), the necessity for vigilance by individuals may be reduced (Berger 1978; Caraco 1979; Lima 1995a), the probability of attack may decline (Berger 1978; Clutton-Brock et al. 1999), and foraging efficiency may increase (Caraco 1979). The existence of these benefits in natural systems suggests a functional advantage to group living. However, group living can cause individuals to incur greater costs. A decrease in vigilance, coupled with an increase in foraging, may result in intense foraging competition (Janson and Goldsmith 1995). In addition, several studies have linked group living with an increase, rather than a decrease, in predation risk through an increased frequency of encountering predators (Taylor 1976; Krause and Godin 1995). Some authors have proposed that the assumed benefits of group living, i.e., decreased vigilance, decreased probability of predation, and increased foraging, reach some maximum and decline thereafter, causing an individual to leave the group (Treisman 1975a, 1975b; Giraldeau 1988).

The influence of predation on group size can be difficult to quantify, especially in species on which successful predation is rarely observed, such as prairie dogs (Hoogland 1981) and primates (Janson

1998). Furthermore, differences between predation rate and predation risk are rarely clarified (Hill and Dunbar 1998; Hill and Lee 1998; Janson 1998). Hill and Dunbar (1998) state that the predation rate is the number of successful predator attacks resulting in mortality, while the predation risk reflects the perceived probability of a predator encounter, based on the cumulative attacks previously experienced by an individual. They propose that the antipredator strategies exhibited by a group of animals reflect predation risk, not predation rate, because animals will respond to both successful and failed predatory attacks. Therefore, by combining three measures, the occurrence of predators, frequency of attempted attacks, and mortality, predation risk may be adequately reflected (Hill and Dunbar 1998; Hill and Lee 1998). In addition, predation risk can be represented as the predation events experienced by a group of animals, as well as the individual predation risk to each animal within the group. The latter can be determined by dividing the total predation events measured by the number of individuals in a group, assuming that risk is equally distributed among all individuals.

Another method of assessing the influence of predation risk on a group, albeit indirectly, is to evaluate the variation in antipredator behaviors across group sizes, namely vigilance (Janson 1998). With respect to group size, the percentage of time spent vigilant per individual theoretically decreases as group size increases (Pulliam 1973; Elgar 1989; Clutton-Brock et al. 1999). Some studies have failed to show a strong relationship between group size and vigilance (Colinshaw 1997; Treves 1998), while others report a strong group-size effect (Caraco 1979; Hoogland 1981). This discrepancy may be a result of inadequate controls of other variables such as environmental conditions, age, and gender-related differences in vigilant behavior (Lima 1987; Elgar 1989). For example, fluctuation of ambient temperature might influence energetic requirements, with lower temperatures imposing a greater demand for foraging (Loughry 1993). Wind velocity could also affect vigilance, particularly in a species like Gunnison's prairie dog (*Cynomys gunnisoni*) that relies on a vocal alarm call system. Furthermore, while the general consensus appears to be that vigilance is an antipredator behavioral strategy, precisely where an animal is scanning when displaying vigilant behavior has been little investigated (Bednekoff and Lima 1998).

We studied the adaptive significance of coloniality in Gunnison's prairie dogs by comparing predation risk and vigilance among colonies consisting of populations of different sizes. The following predictions were tested: (i) adult vigilance will be reduced as population size increases, (ii) individual predation risk for individuals within Gunnison's prairie dog colonies will decrease as population size increases, (iii) if coloniality in Gunnison's prairie dogs is driven by predation pressure as predicted by the predation hypothesis, then vigilance should be used primarily as a mechanism for detecting predators. If vigilance is an antipredator strategy, then vigilant individuals will orient to increase the probability of detecting a predator.

Gunnison's prairie dogs are large, diurnal, highly social ground squirrels whose range is limited to the grasslands of the Colorado Plateau (Hall and Kelson 1959). Gunnison's prairie dogs serve as a good model for assessing vigilance and predation risk in a social group primarily because they are colonial and social and have a well-developed, complex system of alarm calls designed to travel long distances across a colony.

Methods

Study sites and subjects

Our study was carried out at eight Gunnison's prairie dog colonies in the vicinity of Flagstaff, Arizona (elevation 2300 m), from April 2000 to August 2000 (Table 1). The colonies varied in area and population size, but all were located in open alpine meadows surrounded by Ponderosa pines (*Pinus ponderosa*) and exposed to low levels of human traffic. Gunnison's prairie dogs were not captured or marked for

identification during this study. Such disruptions at a colony could have deterred predators and artificially increased vigilance levels.

Table 1. Description of Gunnison's prairie dog (*Cynomys gunnisoni*) colonies used in this study.

Colony	Location	Area (ha)	Estimated population size
Antelope II	35°20'N, 111°51'W	1.44	22
Skunk Canyon	35°08'N, 111°38'W	1.51	56
Little Wing	35°16'N, 111°45'W	4.33	97
Ely	35°11'N, 111°25'W	5.71	250
Hidden Hollow	35°15'N, 111°42'W	6.83	247
State Trust	35°13'N, 111°32'W	22.9	1064
Antelope I	35°21'N, 111°50'W	26.3	1039
Government Knoll	35°19'N, 111°51'W	33.7	960

Data collection

Beginning on 1 April 2000 each colony was sampled once every 10 days for 3 h through 1 August 2000. Colonies were sampled alternately in the morning from 07:00 to 10:00 and in the afternoon from 15:00 to 18:00, the times when prairie dogs were most active (Longhurst 1944; Hoogland 1981), for a total of 24–36 h per colony. A 100-m² area within each colony was selected opportunistically for observations prior to the study, based on viewing ability. Natural terrain features such as rock formations, hills, and trees were utilized for observations. All observations were made using Tasco 8 × 20 binoculars from the same concealed, raised position (≥2 m) behind a portable burlap blind for the duration of the study.

Colony area was determined using a Magellan GPS Tracking Unit and by plotting the perimeter of the colonies on Topo U.S.A. 2.0 computerized mapping software. Once the perimeter was established, properties of integral calculus were used to solve for area.

It is possible to estimate the size of Gunnison's prairie dog populations by assuming that each prairie dog utilizes a minimum of two burrows (Slobodchikoff et al. 1988). Using this method, population size was estimated by counting the active burrows within each observation plot and dividing the number by 2, giving the population density (number/ha) of prairie dogs for each colony. The colony population size was then estimated by multiplying the population density by the colony area. A burrow was considered active if fresh scat was present in and around the burrow opening.

Behavioral data on adult feeding, posting, scanning, moving, aggression, burrowing, grooming, and resting were recorded at 5-min intervals using scan sampling (Altmann 1974). Posting in Gunnison's prairie dogs was identified as a stationary bipedal alert posture, while scanning was identified as quadrupedal scanning of the environment with the head above a 90° angle. Each record of vigilance was scored according to the direction in which each individual was oriented with respect to the colony and included interior, periphery, or undetermined. Sampling began one half-hour after arriving at a colony to allow for habituation. Ambient temperature, wind velocity, and general weather conditions were recorded every half-hour using a Brunton Windwatch, with averages taken for each observation session.

Predation risk was estimated using all-occurrences sampling (Altmann 1974) of the presence of a predator, attempted attacks, and mortality due to predation. Events were summed, regardless of the type of encounter. Two measures of predation risk were used in relevant analyses: (1) the total number of encounters and (2) the number of predation events divided by the estimated population size of each

colony yielded the individual predation risk for that colony: individual risk = number of events /estimated population size.

At the onset of a predation event, all behavioral observations of Gunnison's prairie dogs ceased for the duration of the encounter with the predator. The departure of the predator signaled the end of an event if (i) the predator left the colony and remained absent for 15 min, and (ii) the prairie dogs appeared to resume normal activity. Potential predators of Gunnison's prairie dogs in northern Arizona include coyotes (*Canis latrans*), badgers (*Taxidea taxus*), gray foxes (*Urocyon cinereoargenteus*), red-tailed hawks (*Buteo jamaicensis*), golden eagles (*Aquila chrysaetos*), ferruginous hawks (*Buteo regalis*), rough-legged hawks (*Buteo lagopus*), and harriers (*Circus cyaneus*) (Slobodchikoff et al. 1991).

Data analysis

The percentage of individuals vigilant, P , was calculated for each colony as $P = V_a / N_a$, where V_a is the average number of prairie dogs vigilant for each sampling period and N_a is the average number of prairie dogs observed during each sampling period. The same procedure was utilized for feeding. These values were arcsine-transformed to meet normality assumptions. Because individuals were not marked, there could have been a complex correlation structure among the sequential sampling periods for a given colony, requiring the use of repeated-measures analysis of variance (ANOVA). However, repeated-measures ANOVA is not required when sequential data points within a category have a common covariance structure across categories (SAS Institute Inc. 1995). A test for sphericity was used to test this assumption for vigilance and feeding data in colonies. The results were not significant for vigilance ($\chi^2 = 19.5$, $df = 20$, $p < 0.5$) or feeding ($\chi^2 = 20.9$, $df = 20$, $p < 0.79$), allowing acceptance of the null hypothesis that colonies had the same covariance structures across time. This criterion then allowed us to use univariate analyses of colony identity and sampling date on prairie dog vigilance and feeding.

To evaluate the presence of temporal variation in vigilance and feeding across the study, data were partitioned into two time periods corresponding to before juvenile emergence (1 April – 9 June) and after juvenile emergence (10 June – 7 August). In addition, each sampling date within a colony was assigned a value relative to the date when juveniles appeared. This recoding allowed us to investigate the presence of temporal patterns in vigilant and feeding behavior within each time period. A two-way ANOVA was used to test for significant differences in vigilance among colonies and between time periods, while a multiple regression was used to determine the relationship between vigilance and colony area and differences over time before and after juvenile emergence. The same analyses were repeated for feeding behavior.

There was notable heteroscedasticity in regression residuals involving colony area and population size. Natural-log transformations of these variables virtually eliminated this problem and were used for all analyses. It is possible that the observed variation in population size among colonies was driven by variation in population density. However, a stepwise multiple regression showed that colony area explained 94.8% of the variance in population size, while density explained only an additional 4.9% ($r^2 = 0.99$, $F_{[1,5]} = 1014.9$, $p < 0.0001$). Consequently, estimated population size was used in the analyses.

To test for a relationship between the colony predation risk and population size, \ln predation events was regressed on \ln population size. An advantage of this analysis is that it is also possible to infer how individual risk changed as a function of population size, given how individual predation risk was calculated. If the slope of this allometric regression is significantly less than 1, then individual risk necessarily declines with increasing population size.

Records of vigilance and predation events for each colony were summed over the entire study. A replicated G test was used to test for heterogeneity and determine vigilance type and orientation frequencies (Sokal and Rohlf 1985, box 17.4), while a standard χ^2 test was performed on predation-event frequencies. In addition, the percentage of vigilance that was scanning and posting was regressed on population size. Ambient temperature and wind velocities were measured continuously during the observation period for all colonies. All data analysis was performed using JMP IN Statistical Software Version 3.2.6. The minimum accepted level of significance was $p < 0.05$, except for the multiple analyses on vigilant and feeding behavior. To reduce the likelihood of a Type I error due to the multiple tests performed, a conservative minimum acceptance level of $p < 0.01$ was used.

Results

Environmental factors

The vigilant behavior of Gunnison's prairie dogs did not appear to be influenced by the environmental variables measured in this study. There were no significant differences among the colonies in ambient temperature (ANOVA, $F_{[1,6]} = 0.917$, ns) or wind velocity (ANOVA, $F_{[1,6]} = 4.19$, ns). In addition, vigilant behavior did not differ significantly between morning and afternoon sampling sessions (paired t test: $t_7 = 2.27$, ns), excluding time of day as a factor.

Vigilant and feeding behavior

When vigilance type and orientation were analyzed, the results revealed significant differences in the relative frequency of posting and scanning. Data were homogeneous and there was a significant difference in the frequency of posting and scanning behavior ($G = 33.7$, $df = 1$, $p < 0.001$, $N = 9402$). On average, $55.6 \pm 1.9\%$ (mean \pm SE) of vigilant behavior by Gunnison's prairie dogs recorded in this study was posting. There was no significant relationship between the percentage of posting or scanning and population size (posting: $r^2 = 0.003$, $F_{[1,6]} = 0.02$, ns; scanning: $r^2 = 0.06$, $F_{[1,6]} = 0.41$, ns). Overall, Gunnison's prairie dogs in this study, while engaged in either form of vigilance, were more frequently oriented towards the periphery of the colony ($G = 33.9$, $df = 1$, $p < 0.001$, $N = 9402$) and this accounted for $63.9 \pm 2.65\%$ (mean \pm SE) of all vigilance records.

The percentage of adults vigilant varied significantly among colonies and was significantly higher for the post-juvenile-emergence time period (ANOVA, colony: $F_{[7,73]} = 3.30$, $p < 0.004$; period: $F_{[1,73]} = 8.31$, $p < 0.005$; Fig. 1). Results suggested that the two smallest colonies were driving the variation observed and once these were removed, colony differences were no longer significant (ANOVA, colony: $F_{[5,54]} = 0.58$, ns). Vigilance decreased significantly as a function of increasing area, as well as over time before and after juvenile emergence (whole model, $r^2 = 18.1$, $F_{[2,79]} = 8.75$, $p < 0.0004$; ln area: $F_{[1,79]} = 7.69$, $p < 0.007$; sampling day: $F_{[1,79]} = 8.71$, $p < 0.004$; Fig. 2). However, the decrease in vigilance as a function of colony area was attributable to the high proportion of individuals vigilant in the two smallest colonies. Removing them from the analysis rendered the ln area effect nonsignificant ($F_{[1,59]} = 0.52$, ns).

The percentage of individuals feeding varied significantly among colonies and was significantly lower for the post-juvenile-emergence time period. However, a significant interaction was present, suggesting that the effect of pre- and post-juvenile-emergence time periods on feeding showed a different pattern depending on the colony (ANOVA, colony: $F_{[7,65]} = 2.97$, $p < 0.009$; period: $F_{[1,65]} = 11.96$, $p < 0.001$; interaction: $F_{[7,65]} = 4.02$, $p < 0.001$). Colony area had no significant relationship to the percentage of individuals feeding, but feeding increased significantly over time before and after juvenile emergence (whole model, whole model: $r^2 = 13.3$, $F_{[2,78]} = 5.99$, $p < 0.004$; ln area: $F_{[1,78]} = 0.19$, ns; sampling day: $F_{[1,78]} = 11.9$, $p < 0.0009$).

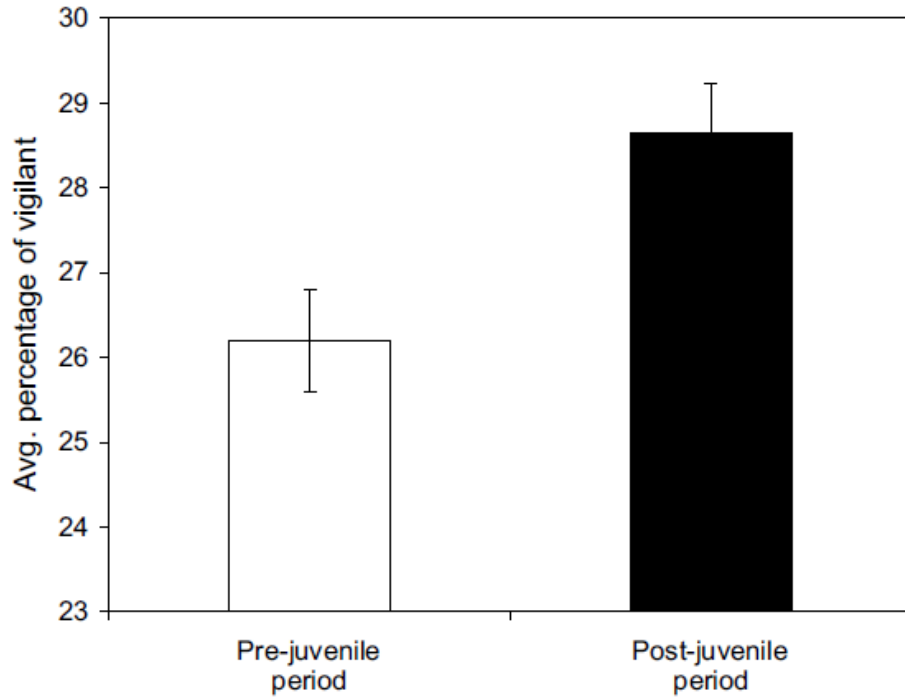


Fig. 1. Average proportions of Gunnison's prairie dogs (*Cynomys gunnisoni*) vigilant (mean \pm SE) during the pre- and postjuvenile-emergence time periods.

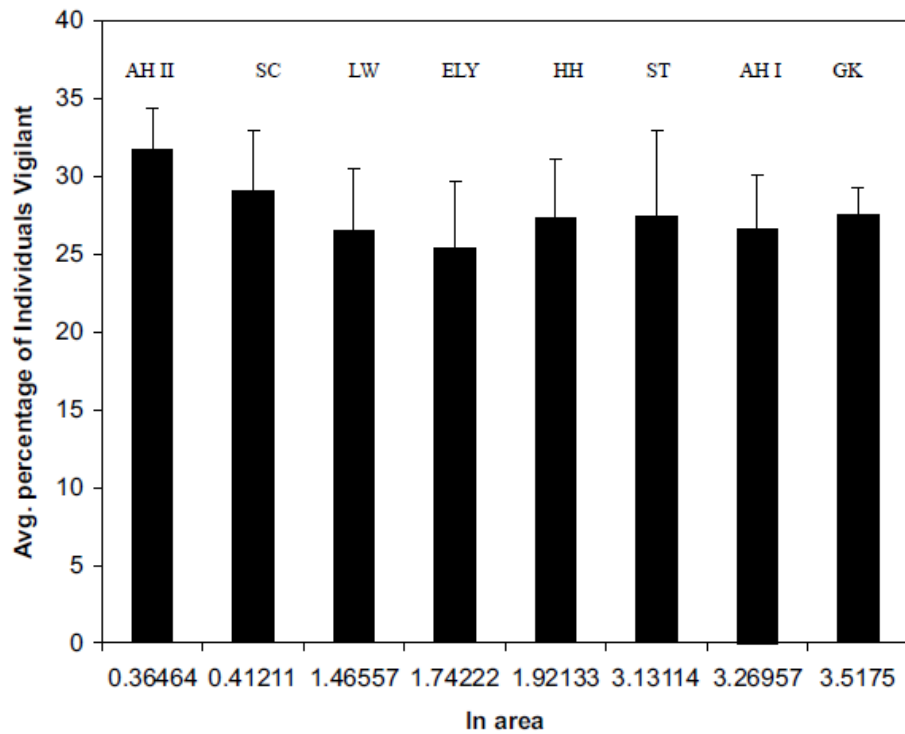


Fig. 2. Average proportions of individuals vigilant (mean \pm SE) as a function of colony area. Colonies are identified as follows: AH II, Antelope Hill II; SC, Skunk Canyon; LW, Little Wing; ELY, Ely; HH, Hidden Hollow; ST, State Trust; AH I, Antelope Hill I; GK, Government Knoll.

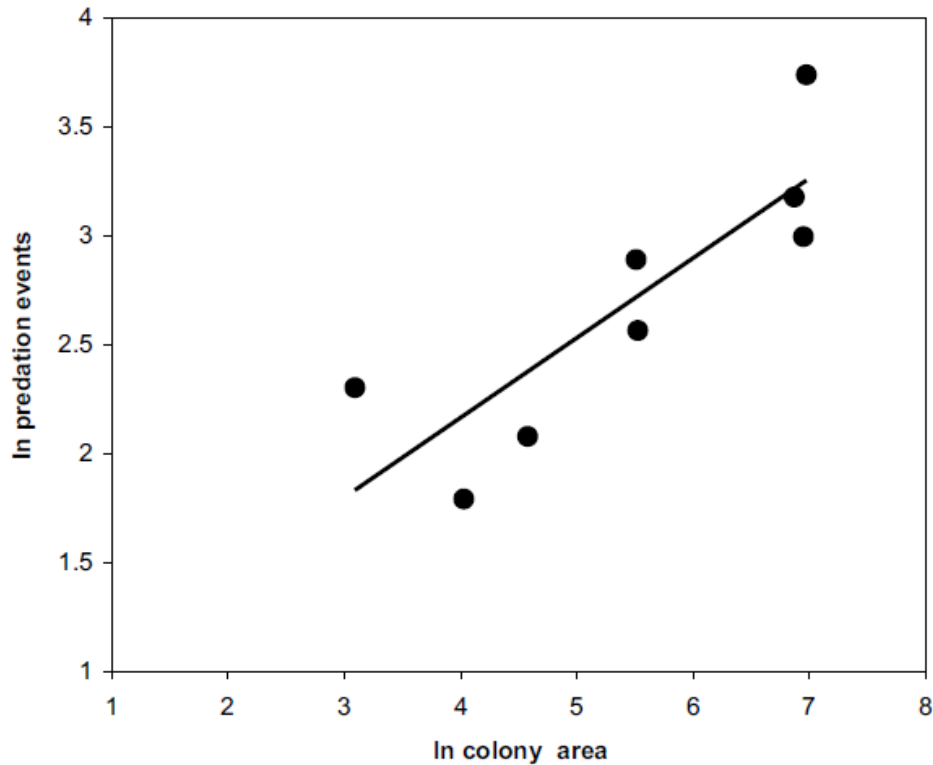


Fig. 3. Effect of population size on actual predation risk, i.e., the number of predation events per colony over the study period (linear regression: $y = 0.69 + 0.37x$).

Predation risk

Although larger colonies had an increased frequency of predator encounters, individuals in larger colonies experienced a lower individual predation risk. Linear regression analysis revealed a highly significant positive relationship between the number of predator encounters and population size ($r^2 = 0.71$, $F_{[1,6]} = 13.4$, $p < 0.01$; Fig. 3). The slope of this regression was significantly less than 1 ($t_{[6]} = 5.96$, $p < 0.001$). Dividing both sides of the regression equation by population size yields the following equation for individual predation risk as a function of population size: individual predation risk = $2.01 \times$ population size -0.633 . Thus, as population size increased, the per-capita predation risk decreased (see Table 2 for individual values).

Predation

Table 2 provides a detailed description of predation events for each Gunnison's prairie dog colony over the study period and the corresponding predation risk to each prairie dog. A total of 142 predation events occurred, of which 16.2% resulted in an attempt to capture a prairie dog. In total four kills were observed, so 17.4% of all attempts were successful. Aerial predators were responsible for 74% of all attacks undertaken; hawks killed three prairie dogs, resulting in a 17.6% success rate. Though terrestrial predators occurred less frequently, attacked less often, and made a single kill over the study period, the calculated success rate is similar to that of aerial predators at 16.7%.

Table 2. Distribution of predator encounters, numbers of successful kills, types of predator, and individual predation risk.

Colony	Estimated population size	No. of encounters	No. of kills	Predator type	Individual risk
Antelope II	22	10	1	Hawk*	0.45
Skunk Canyon	56	6	0	Hawk	0.11
Little Wing	97	8	0	Coyote; hawk; badger	0.08
Hidden Hollow	247	18	0	Coyote; hawk	0.07
Ely	250	13	0	Hawk	0.05
State Trust	1064	42	1	Hawk*	0.04
Government Knoll	960	24	0	Hawk; badger	0.03
Antelope I	1039	20	2	Coyote*; hawk*; fox	0.02

*Successful kill.

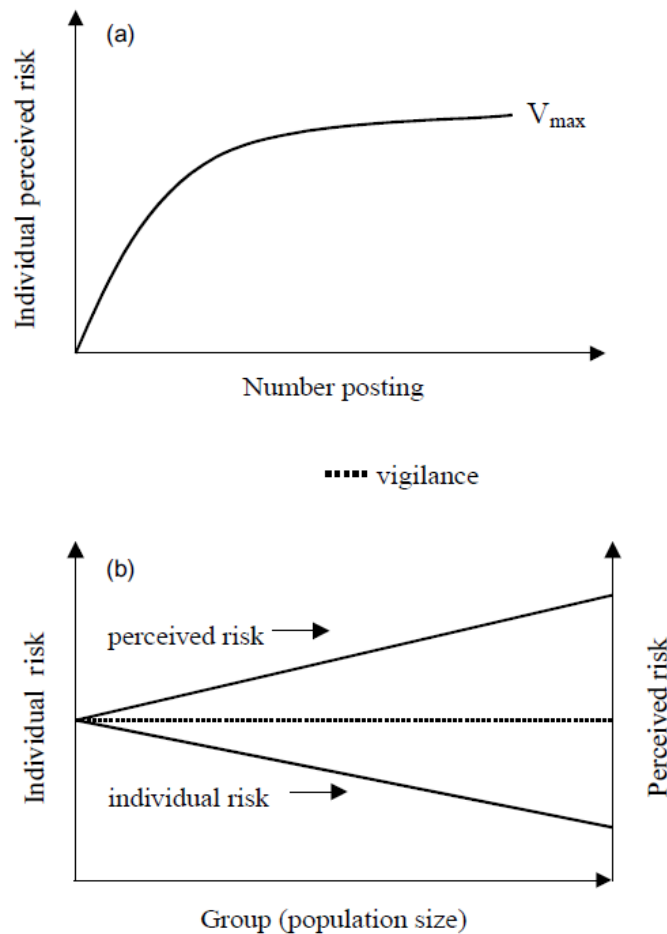


Fig. 4. (a) Additive effect of an increase in the number of individuals posting. As the number of posting individuals increases, the predation risk perceived by others increases until a maximum state of vigilance (V_{max}) is achieved. (b) As group size increases, the perceived predation risk (based on the number of Predation events) also increases, while individual risk decreases. Both of these functions are independent of proportion of individuals vigilant.

Discussion

As predicted, and in accordance with the dilution model first proposed by Galton (1883) and subsequently expanded by others (Hamilton 1971; Vine 1971; Pulliam 1973), Gunnison's prairie dogs in larger populations experienced a lower individual predation risk. A reduced individual predation risk in larger groups has also been reported for other mammals (hoary marmots (*Marmota caligata*), Holmes 1984; blacktailed prairie dogs (*Cynomys ludovicianus*), Devenport 1989; Dall's sheep (*Ovis dalli*), Frid 1997). Protection by dilution relies on the assumption that the predation rate cannot increase faster than the size of a given group (Lima 1995b). Hamilton's (1971) model predicts that animals will favor grouping even if predation occurs at a higher rate as groups get larger, although the magnitude of the benefits will level off as group size continues to increase.

Across several species, a trend has been observed which suggests that larger groups have a higher predator-encounter rate (Page and Whitacre 1975; Krause and Godin 1995). Similar results were obtained in this study, where larger Gunnison's prairie dog colonies had a significantly higher predator-encounter frequency. However, the increase in predator encounters across population sizes was not enough to nullify the benefit of a decreased individual risk by dilution. It should be noted that these results do not take into account differences in local predator density, the influence of different home ranges of various predators, or feeding requirements of predators, all of which can have an impact on how often a given colony encounters a predator.

Animals in larger groups may also benefit from enhanced predator detection and reduced individual vigilance, allowing animals to forage more efficiently (Bertram 1978). A number of empirical studies have shown a negative linear relationship of vigilance to group size, as well as enhanced predator detection, supporting the detection model (Berger 1978; Hoogland 1981; Lima 1995b). In our study, the hypothesis that vigilance would be reduced as population size increased was supported. However, this variation was driven entirely by the two smallest colonies, Skunk Canyon and Antelope Hill 2. In contrast, feeding showed no relationship to increasing population size, suggesting that the vigilant behavior of Gunnison's prairie dogs is not a result of a vigilance–foraging trade-off.

In prairie dogs, it is possible that for larger groups, vigilant behavior is independent of group size and is based primarily on perceived predation risk, which can greatly exceed an individual's risk (Lima and Dill 1990). This perceived risk might arise from prairie dogs monitoring the behavior of other individuals in the colony. The bipedal posting stance can alert others to a source of potential danger. Figure 4a illustrates a hypothetical situation whereby, during a random scan event, an individual Gunnison's prairie dog may be alerted to danger by observing another group member posting and, subsequently, may opt to post itself. As the number of predation events increases, an individual's perceived risk may correspondingly increase. If posting serves as a signal of potential danger, and the probability of posting increases with the number of individuals posting, the perceived predation risk for an individual would increase until a maximum state of vigilance is achieved. This maximum level of vigilance can be represented as all individuals being vigilant simultaneously, or an individual being as vigilant as possible given the energy available to it for expending.

If vigilance levels are constrained by a maximum threshold, and larger groups reach this threshold rapidly because of an increase in perceived risk, then membership in a group would not necessarily reflect a vigilance–foraging trade-off. Under a greater perceived predation risk, group membership would instead reflect an appropriate compromise between perceived and actual predation risk that is independent of vigilance. Figure 4b illustrates how constant levels of vigilance, such as those observed in this study, can occur. As group size increases, the number of predation events increases, resulting in a corresponding increase in perceived risk. However, this effect is countered by a reduction in individual risk as group size

increases. The difference between perceived risk and individual risk may result in constant levels of vigilance beyond the smallest group sizes.

Vigilant behavior may also be influenced by group size if individuals increase vigilance in response to the presence of more conspecifics (Treves 1998). An underlying assumption of the model presented here is that Gunnison's prairie dogs monitor the behavior of conspecifics, and that detecting intruders and detecting predators are not mutually exclusive properties of vigilance. Furthermore, if one assumes that posting serves an antipredator function, while scanning reflects social vigilance, the lack of a significant relationship of either to population size suggests that an increase in the number of conspecifics plays a minimal role in prairie dog vigilant behavior.

The models presented here suggest that feeding will remain at relatively fixed maximum levels that are independent of group size, as was observed in our study. Furthermore, while the proportion of individuals vigilant is higher when groups are small, the benefits of reduced vigilance with increasing group size rapidly reach a maximum threshold. Overall, these results suggest that Gunnison's prairie dogs are not more or less vigilant at the expense of feeding as predicted by the detection model. Instead, they appear to trade off actual individual predation risk against perceived predation risk.

Acknowledgments

We thank the United States Forest Service, Peaks Ranger District, for permission to conduct research in Coconino National Forest, the Arizona State Land Department, and Mr. and Mrs. Karl Ely for the use of their prairie dog colonies. We are especially grateful to field assistants Matthew Husband and Bianca Perla for their help with this project. Lastly, we thank Drs. Peter Bednekoff, Lee Drickamer, Charles Janson, and Bernadette Marriott and two anonymous reviewers, whose comments greatly improved the manuscript.

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