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WHY ARE UTAH PRAIRIE DOGS VIGILANT?

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Detection of predators, social monitoring, and avoidance of infanticide have been invoked to explain patterns of vigilance. To test these hypotheses, I examined the vigilance of 120 Utah prairie dogs (*Cynomys parvidens*) using ''one–zero'' sampling on individuals of known sex, reproductive state, and genealogy. Male and female prairie dogs increased vigilance during periods of heightened predation risk (i.e., with few surrounding conspecifics) unless the risk resulted from spatial positioning in the colony. Reproductive males and females were more vigilant than their nonreproductive counterparts during breeding, and estrous females increased vigilance in the presence of prospective mates. In contrast to predictions of the infanticide-avoidance hypothesis, lactating females were less vigilant than females without litters when neonates were in a nursery burrow and vulnerable to infanticide by males. Males were more vigilant than females, but not when the offspring of their sexual partners were vulnerable to infanticide or opportunities to kill offspring increased. I conclude that vigilance in Utah prairie dogs varies mostly in relation to the risk of predation. Mate competition also increases vigilance in males and females. However, prevention or facilitation of infanticide does not appear to influence vigilance in males or females.

Key words: *Cynomys*, detection, group-size effect, infanticide, lactation, mate guarding, prairie dog, predation, social monitoring, vigilance

Gregarious animals detect threats to themselves or their kin through antipredator vigilance (visual scanning of areas beyond the immediate vicinity for predators or warning signals from conspecifics—Lima 1995; McNamara and Houston 1992; Vine 1971). According to theoretical models of antipredator vigilance based on the observations of Galton (1871), group living is advantageous to individuals that are susceptible to predation for 2 reasons. First, increases in the number of individuals (''group size'') heighten vigilance within groups, thus making predator detection likely (Pulliam 1973). Second, increases of group size reduce predation risk to individuals through selfish herd effects and risk dilution (Hamilton 1971; Lima 1995). It follows from Hamilton's (1971) predictions that individuals with many neighboring conspecifics should reduce their vigilance, and support for this notion comes from myriad avian and mammal species (e.g., Elgar 1989; Quenette 1990). Furthermore, individuals increase vigilance in positions of higher predation risk, such as at the periphery of a group where there are few neighboring conspecifics (e.g., Burger and Gochfield 1994; Rose and Fedigan 1995).

Animals can be vigilant for reasons other than detection of predators. For example, mate defense occurs in squirrels (e.g., Hoogland 1995) and primates (e.g., Hrdy 1977; Rose and Fedigan 1995) when males monopolize females so they cannot copulate with additional males. That vigilance by males is influenced by mate defense is suggested by studies where individuals monitor competitors (e.g., Cresswell 1997; Slotow and Rothstein 1995) or guard copulatory partners (e.g., Baldellou and Henzi 1992; Davis and Brown 1999). In contrast, estrous females may maximize reproductive success by copulating with more than 1 partner or selecting the most robust partner (e.g., Hoogland 1998a). Influences of female mate choice and promiscuity on vigilance are suggested for Belding's ground squirrels (*Spermophilus beldingi*) that watch aggressive bouts between males and choose a mate according to previous copulatory successes or fighting ability (Sherman 1976). Social monitoring may therefore be an applicable hypothesis to explain vigilance, even when individuals are vigilant to deter predation.

Social monitoring (rather than predation) can sometimes be a predominant influence on vigilance when certain costs of coloniality are high (e.g., competition for mates or misdirected parental care) or if predation risk is low. The evolution of vigilance for social monitoring was predicted by King (1955) for black-tailed prairie dogs (*Cynomys ludovicianus*) because of the rigorous competition for mates within colonies. Although examination of subsequent data on prairie dogs suggests that vigilance functions primarily to prevent predation (Hoogland 1979), results from some primates support King's (1955) hypothesis (Hirsch 2002; Treves 2000).

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Social monitoring may encompass females defending young from infanticide as well as intrasexual mate competition. Steenbeek et al. (1999) predicted risk of infanticide to be an additional indicator of vigilance in male and female Thomas's langurs (*Presbytis thomasi*) because of the high costs of infant loss. Further, they predicted that males could influence the distribution of females via infanticide, and that females could reduce this risk if they associated with a solitary male. Female ground squirrels live in kin clusters around territorial males and female protection of young from infanticide has been suggested by field observations (e.g., Balfour 1983; Hoogland 1995; King 1955; McLean 1984; Sherman 1980), but a relationship between risk of infanticide and vigilance has not been formally tested. The purpose of this study was to assess the influence of detection of predators, competition for mates, and avoidance of infanticide on vigilance by the Utah prairie dog (*Cynomys parvidens*).

Study animal.—Utah prairie dogs are colonial, diurnal, herbivorous, ground-dwelling squirrels that hibernate during severe winter weather (Hoogland 2001, 2003, in press; Hoogland et al. 2004, 2006; Stebbins 1971). They form social breeding groups (clans) that contain several philopatric females of close kinship, their young, and 1 or 2 nonreproductive yearling males. Clans maintain exclusive territories that are defended by female kin across generations. Females are reproductive at 1 year of age, whereas males can be reproductive at 1–2 years of age. Length of gestation is usually 29 or 30 days. Lactation occurs for about 38 days before juveniles emerge from their natal burrows, and usually continues (often communally among clan mothers) for another 1–2 weeks.

During a 3-week breeding season (late March to early April), reproductive males gain the opportunity to copulate by emerging victorious in competitions to become the sole male associated with particular clans of females. When a female comes into estrus (1 day per year), she may seek extra copulations with males from adjacent clans if not guarded well by the male clan member (see Hoogland 1998a). Cuckoldry occurs when males invade adjacent clans that are associated with other males and copulate with females (see Haynie et al. 2003; Hoogland 1995).

Hoogland (in press) concluded that for Utah prairie dogs, infanticidal males become residents of the territory in which killing occurs after emigrating from another clan or colony (48/48 = 100%). Killing and cannibalism usually occur aboveground after a male emerges from a nursery burrow with a live unweaned juvenile (45/48 = 94%). Marauders are of 3 types: male that copulated with the victimized mother ($n = 9$), breeding male that did not copulate with the victimized mother ($n = 19$), and nonbreeding yearling male ($n = 20$). Marauders usually kill only 1 juvenile within a litter ($n = 22$ different killers), but occasionally eliminate an entire litter via serial infanticides over several days ($n = 3$).

Predictions.—The predator-detection hypothesis predicts that individual vigilance will increase when predation risk is heightened, that is, when there are few neighboring conspecifics, including when an individual is located on the colony periphery rather than in its center. Because individuals that have relatives watchful for predators in their immediate area are probably less likely to be killed by a predator, a group-size effect should also exist within clans. In contrast, if awareness of conspecifics is the predominant reason for vigilance, then prairie dogs should increase vigilance in the presence of many neighboring conspecifics, and in the center of colonies rather than the periphery, in contradiction to the predator-detection hypothesis.

Although the predictions of the predator-detection and social-monitoring hypotheses are mutually exclusive, both are compatible with individuals monitoring conspecifics in particular situations. If Utah prairie dogs watch conspecifics to increase their opportunity to mate, then appropriate predictions are that reproductive individuals should be more vigilant than nonreproductive individuals, the difference should occur mostly during breeding, and the difference should occur in the presence of individuals from adjacent clans that are likely copulatory partners or competitors. Therefore, these predictions can apply to males preventing cuckoldry or looking for pre-estrous females as well as estrous females observing prospective mates. According to the infanticide-avoidance hypothesis, nursing females should increase vigilance during lactation and in the presence of conspecifics that are likely to commit infanticide (i.e., any males that fit the criteria of ''potential marauders,'' listed above). Under this hypothesis, nursing females should also decrease vigilance after the loss of their litters.

Males are more vigilant than females in many species (Baldellou and Henzi 1992; Rose and Fedigan 1995), usually because of constraints on females during lactation and pregnancy (see Clutton-Brock et al. 1989). If the infanticide-avoidance hypothesis is applicable, then nursing females may be more vigilant than males (reproductive and nonreproductive), but not if males increase vigilance to look for opportunities to commit infanticide while neonates are underground. On the other hand, Steenbeek et al. (1999) suggested that if males are likely to have sired the young in a social group, they might increase vigilance to protect their young by detecting intruding males that may be marauders (see also McLean 1983). If this notion is supported for Utah prairie dogs, then perhaps nursing females within a clan should relax their vigilance in the presence of the male associated with the clan.

Like other investigators (Hoogland 1979), I ignore possible effects of food competition on vigilance during my test of these predictions (e.g., Arenz and Leger 1999; Carey and Moore 1986) because family groups of prairie dogs have minimal overlap and scramble competition is unlikely (see also Randler 2005).

Materials and Methods

Five trained colleagues and I studied wild, free-ranging Utah prairie dogs of known genealogies from 8 March 2004 to 9 July 2004 at the Mixing Circle Colony (4.25 ha) in Bryce Canyon National Park, Utah (about 2,600 m elevation). The colony size ranged from 112 to 125 prairie dogs during the study.

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Environmental conditions and vegetation at the site have been described previously (e.g., Bryant 1996; Roberts et al. 1992; Stebbins 1971). Potential predators of the prairie dogs included American badgers (*Taxidea taxus*), coyotes (*Canis latrans*), long-tailed weasels (*Mustela frenata*), red foxes (*Vulpes vulpes*), gray foxes (*Urocyon cinereoargenteus*), northern goshawks (*Accipiter gentilis*), golden eagles (*Aquila chrysaetos*), and prairie falcons (*Falco mexicanus*—Hoogland et al. 2006).

We assigned individuals to the same clan if they participated in the defense of the same territory and if they spent the night in the same territory (Hoogland 1995). Behavioral interactions also helped to identify members of the same clan, because, like black-tailed and Gunnison's prairie dogs (*Cynomys gunnisoni*—Hoogland 1995, 1998a, 1998b), intraclan interactions were more amicable than interclan interactions. We determined territorial boundaries of clans by mapping territorial disputes between individuals of different clans, and from interactions and feeding sites of individuals of the same clan (Hoogland 1995).

We examined the vigilance of 120 adult and yearling Utah prairie dogs. Clan memberships were known for 97 of these individuals ($n = 23$ clans). Results come from 76 reproductive females, 32 of these females during their estrus, 29 reproductive males, and 15 nonreproductive yearling males. When tests concern females that lost their litter, results contain data from 15 of the 76 reproductive females that stopped lactating after the death of their entire litter via predation, infanticide, apparent disease, or unknown reasons.

The reproductive cycle.—Using the methods of Hoogland (1995), we captured all adult and juvenile residents at the study site and marked them distinctively with Nyzanol dye (Greenville Colorants, Clifton, New Jersey). We always arrived at the study site before the prairie dogs started to rise aboveground that day, and remained there until the last individual had submerged for the night. We logged more than 1,500 h of field observations per person, all from 4-m-high observation towers.

Like Gunnison's and black-tailed prairie dogs (Hoogland 1995, 1997), Utah prairie dog mothers give birth underground. We inferred parturition, and simultaneously confirmed conception and pregnancy, from a noticeable increase in the time spent in the home nursery burrow as determined from observing last submergences (Hoogland 1997).

We considered males to be reproductive if they had a pigmented scrotum or descended testes. For females, we observed the appearance of the vulva (i.e., fully opened) to determine whether individuals were in estrus. Females were sexually receptive on a single day of the breeding season, and most consortships occurred underground. We therefore inferred consortships from aboveground diagnostic behaviors that happened only on the day of mating (see Hoogland 1995, 1998b; Hoogland and Foltz 1982): observation of a male and female submerging in the same burrow and remaining there together for more than 10 min; self-licking of the genitals by both sexual partners; mutual dust-bathing and grooming by both partners; frequent amicable interaction of reproductive males with the estrous female; a postejaculation mating call given by the copulating male; and late final submergences (often in the same burrow) of both sexual partners. Occasional aboveground copulations also revealed these behaviors, and the dates of inferred parturition and 1st aboveground appearance of a mother's offspring varied directly with the mother's alleged date of copulation.

We considered females to be nursing after parturition was inferred. When a female stopped sleeping in her natal burrow, we suspected loss of the litter and the female was trapped to determine whether she had ceased lactating from her nipple condition (i.e., flat and dry—Murie and Harris 1982; Sherman 1981).

Our methods followed guidelines of the American Society of Mammalogists for animal care and use (Animal Care and Use Committee 1998), and were approved by the Institutional Animal Care and Use Committee at the University of Maryland.

Quantification of individual vigilance.—I defined a vigilant posture as an upright stance, apparently to search for predators or conspecifics, or an upward tilted head while on top of a burrow mound or feeding (see Clark 1977). I defined all other activities or postures (e.g., feeding with head downward, socializing, excavating, and grooming) as nonvigilant behavior. Every half hour, my colleagues and I sampled individuals at 5-s intervals repeatedly and scored them as vigilant or nonvigilant according to a ''one–zero'' sampling method (Martin and Bateson 1993). Sampling continued for 3 min. Wherever possible, we recorded the position within the group (central or peripheral) of the individual. We scored an individual as central if they resided in a clan where >50% of the clan territory boundary was contiguous with the boundaries of other territories, and as peripheral if <50% of the clan territory boundary abutted other territories (Hoogland et al. 2006).

We sampled females 4 times over a 12-h period during their estrus. Otherwise, individuals were randomly selected within 2 constraints. First, some individuals were farther away from observation towers than others or were more inconspicuous because of vegetation. Second, it was necessary to counterbalance the observations across different times of day to minimize time of day effects. If these qualifications disqualified an individual we selected, we moved to another randomly selected individual. With the exception of estrous females, individuals were not sampled more than twice a day. We analyzed more than 510 h of data from 10,208 three-minute samples involving 120 individuals (median: 83.3 samples per individual, range: 30–152 samples). We also scored the time between 1st daily emergence and the 1st time an individual engaged in more than 5 s of nonvigilant activity (described above). We recorded 817 of these ''lag times'' from 62 individuals ranging from less than 1 to 69 min.

We measured group size and the presence of particular individuals at different times of day in different clans using 2 methods. First, we observed clans from dawn until dusk, and recorded the 1st daily emergence (or 1st time seen) and last daily submergence (or last time seen) of all individuals. Individual Utah prairie dogs and their clan members emerge for activity at different times, and are vigilant before commencing

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foraging activities. Particularly during morning, group size varies because some individuals (and clans) emerge while others are not yet aboveground (Hoogland 1979). Second, we recorded all aboveground (i.e., ''active'') individuals in the colony area every half hour (Hoogland 1995; Martin and Bateson 1993).

We noted all predator sightings and alarm calls by prairie dogs (Hoogland et al. 2006). Because alarm calls might elicit increased levels of vigilance (e.g., Baldellou and Henzi 1992; Hirsch 2002), and disturbances in an area typically cause all prairie dogs there to become vigilant (Hoogland 1995), we only recorded data in the absence of calling or predators (15 min after the last disturbance).

To reduce the possibility that observations could be influenced by responses to human observers, we only recorded vigilance data 15 min after entering an observation tower (Hoogland 1979). I did not adjust for differences in data collection among the 6 different observers, because the differences I found in the percentage of samples recorded as vigilant between observers were not statistically significant ($P = 0.72$, Kruskal–Wallis analysis of variance [ANOVA]).

Data analysis.—I calculated the time allocated to vigilance for each individual as the percentage of all 5-s intervals during which 1 or more vigilant postures occurred (Steenbeek et al. 1999). I also calculated average lag times for each individual. I calculated vigilance and average lag times for different positions in the group (central versus peripheral), and different numbers of active conspecifics (within the entire colony and individual clans).

Because individuals lived and foraged in different parts of the colony, I tested for edge effects using unpaired *t*-tests of vigilance and average lag times for central or peripheral positioning. I determined whether individuals increased or decreased vigilance with more conspecifics present using regressions of average lag times and vigilance against the number of conspecifics present in the colony and clan.

I sorted data on vigilance and lag times into 5 categories to test the effects of sex and reproductive state on vigilance (reproductive male, nonreproductive male, reproductive female, female that lost litter, and estrous female). To determine the effects of the annual reproductive cycle on vigilance, I classified samples as follows: breeding—samples that occurred before the last female estrus (for males) or before an individual's estrus (for females); pregnancy—samples that occurred during the time between estrus and parturition for individual females (I also recorded male vigilance during these periods for comparison); lactation—samples that occurred after the 1st parturition in the colony (for males), or individually according to the time of parturition (for females; this was appropriate because once neonates were present underground, males had the opportunity to commit infanticide); and estrus—samples that occurred during the day of receptivity for females only.

Because every studied female copulated and apparently became pregnant, I pooled all samples on females until lactation commenced, with the exception of estrous days. I used ANOVA and either paired or unpaired *t*-tests (as appropriate) to determine the effects of conspecific presence and phase of the reproductive cycle on individuals that differed in sex and reproductive state. After lactation commenced, I distinguished between nursing females and the 15 females that lost their litters. I also compared these 15 females before and after the loss of their litters using a paired *t*-test.

For several reasons, sample sizes for seemingly related or similar analyses were not always identical. Sometimes individuals died during the period of analysis, for instance, or were not sufficiently active to supply enough focal samples to be included in the comparison. I always excluded individuals that did not contribute at least 3 focal samples to the comparison.

Analyses were performed using MINITAB software (version 13.32; Minitab Inc., State College, Pennsylvania). I tested for normality with Kolmogorov–Smirnov tests. I considered samples independent if from different individuals, but not if from different one–zero samples on the same individual (Machlis et al. 1985). The number of individuals in the sample (n) also is given. Values are presented as means ± 1 *SE*. All results reflect 2-tailed tests that assume equal variances; comparisons are considered significant if $P < 0.05$.

Results

Individuals that were active on the periphery were not significantly more vigilant than their central counterparts with respect to lag times (7.1 ± 0.6 min versus 7.2 ± 0.6 min; $t = 0.71$, $d.f. = 44$, $P = 0.39$) or vigilance (36.7% ± 2.8% versus 38.8% ± 2.2%; $t = 0.21$, $d.f. = 58$, $P = 0.28$). When I analyzed individuals separately according to sex and reproductive status, the results were similar; position in the group (peripheral versus central) did not influence vigilance in reproductive males (46.4% ± 2.3% versus 45.0% ± 2.9%; $t = 0.79$, $d.f. = 13$, $P = 0.21$), nonreproductive males (41.9% ± 1.8% versus 41.6% ± 1.7%; $t = 0.13$, $d.f. = 8$, $P = 0.44$), reproductive females (30.9% ± 1.3% versus 30.3% ± 1.0%; $t = 0.47$, $d.f. = 22$, $P = 0.22$), or females that lost their litter (34.2% ± 4.4% versus 38.3% ± 4.0%; $t = 0.98$, $d.f. = 9$, $P = 0.13$).

Because the number of active individuals in the colony did not correlate with either the number of individuals or percentage of individuals active in the 23 known clans ($r^2 < 0.50$ for all comparisons), I considered the effects of conspecific presence within the clan and the colony separately. The overall analysis showed that individuals were more vigilant and had longer lag times when fewer colony members were active ($r^2 = 0.92$, $P = 0.019$ and $r^2 = 0.74$, $P = 0.0083$, respectively; Fig. 1); when I analyzed individuals separately according to sex and reproductive status, the results were almost identical. Individuals were more vigilant and had longer lag times when fewer clan members were active ($r^2 = 0.92$, $P = 0.026$ and $r^2 = 0.83$, $P = 0.034$, respectively; Fig. 2).

Reproductive males were more vigilant and had longer lag times during breeding than did nonreproductive males ($t = 2.3$, $d.f. = 42$, $P = 0.012$ and $t = 2.1$, $d.f. = 21$, $P = 0.018$, respectively; Figs. 3a and 3b); this trend was not significant

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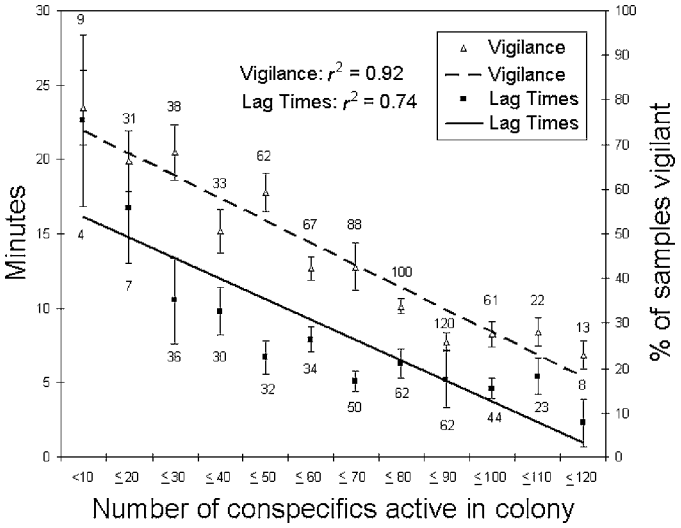


Fig. 1.—The relation of percentage of samples in which subjects were vigilant and average lag times to the number of conspecifics active in the colony. The numbers at the data points represent the number of individuals in the sample.

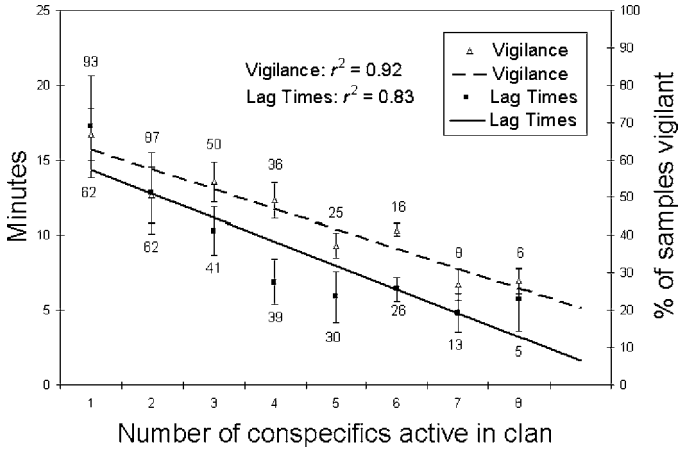


Fig. 2.—The relation of percentage of samples in which subjects were vigilant and average lag times to the number of conspecifics active in the clan. The numbers at the data points represent the number of individuals in the sample.

directly after breeding (i.e., after all females had become pregnant). Reproductive males were more vigilant and had longer lag times during breeding than during female pregnancy ($t = 2.0$, $d.f. = 25$, $P = 0.036$ and $t = 2.3$, $d.f. = 11$, $P = 0.025$, respectively) and lactation ($t = 1.8$, $d.f. = 25$, $P = 0.021$ and $t = 2.0$, $d.f. = 11$, $P = 0.016$, respectively).

For all 29 reproductive males in the colony, I recorded vigilance with different numbers of pre-estrous females (i.e., possible mates) and reproductive males in adjacent clans (i.e., competitors) that were active (Fig. 4). Vigilance varied with the number of reproductive males present (ANOVA: $F = 2.7$, $d.f. = 3, 112$, $P = 0.033$) but not the number of pre-estrous females (ANOVA: $F = 1.2$, $d.f. = 3, 112$, $P = 0.24$); vigilance was higher when 1 reproductive male in an adjacent clan was active rather than none ($t = 2.6$, $d.f. = 27$, $P = 0.0083$), but was not higher when multiple rather than single males were active (1 versus 2 males: $t = 1.0$, $d.f. = 27$, $P = 0.37$; 2 versus >2 males: $t = 0.94$, $d.f. = 27$, $P = 0.45$; Fig. 4).

For 32 estrous females, I recorded vigilance with different numbers of reproductive males in adjacent clans (i.e., possible mates other than the male associated with their clan) that were active. Estrous females were more vigilant than anestrous females in their clan (36.3% ± 2.3% versus 25.0% ± 4.0%; $t = 2.5$, $d.f. = 48$, $P = 0.0034$); furthermore, estrous females were more vigilant with 1 reproductive male in an adjacent clan active than none (40.2% ± 3.4% versus 34.2% ± 3.5%; $t = 8.3$, $d.f. = 30$, $P = 0.031$). Estrous females were not significantly more vigilant with 2 or >2 active reproductive males in adjacent clans than with one ($t = 0.83$, $d.f. = 30$, $P = 0.35$ and $t = 1.0$, $d.f. = 30$, $P = 0.22$, respectively).

Figures 3a and 3b show that reproductive females did not increase vigilance or have longer lag times after giving birth (ANOVA: $F = 0.52$, $d.f. = 2, 222$, $P = 0.34$ and $F = 2.2$, $d.f. = 2, 84$, $P = 0.14$, respectively). Females were not significantly more vigilant and did not have longer lag times during lactation than during pregnancy ($t = 0.76$, $d.f. = 72$, $P = 0.42$ and $t = 0.81$, $d.f. = 27$, $P = 0.53$, respectively) and were less vigilant and had shorter lag times after giving birth than during breeding season ($t = 1.8$, $d.f. = 72$, $P = 0.30$ and $t = 1.9$, $d.f. = 27$, $P = 0.36$, respectively). Furthermore, lactating females were not more watchful than females that were no longer nursing (Figs. 3a and 3b); indeed, females that lost their litter were more vigilant in both the overall (36.4% ± 2.4% versus 30.4% ± 1.9%; $t = 4.0$, $d.f. = 87$, $P = 0.0024$) and the paired comparison (36.4% ± 2.4% versus 30.2% ± 2.1%; $t = 2.0$, $d.f. = 13$, $P = 0.0043$) and had longer lag times in both the overall (6.9 ± 1.6 min versus 4.1 ± 0.8 min; $t = 1.7$, $d.f. = 37$, $P = 0.022$) and the paired comparison (6.9 ± 2.0 min versus 3.4 ± 1.6 min; $t = 2.1$, $d.f. = 7$, $P = 0.021$).

Neither lactating females nor females that lost their litter increased vigilance (ANOVA: $F = 1.1$, $d.f. = 3, 292$, $P = 0.35$ and $F = 1.3$, $d.f. = 3, 56$, $P = 0.44$, respectively) or had longer lag times (ANOVA: $F = 1.8$, $d.f. = 3, 112$, $P = 0.41$, and $F = 1.4$, $d.f. = 3, 32$, $P = 0.46$, respectively) with more potential marauders present (Figs. 5a and 5b).

Lactating females and females following loss of litters did not have significantly shorter lag times ($t = 0.78$, $d.f. = 27$, $P = 0.34$ and $t = 0.65$, $d.f. = 7$, $P = 0.52$, respectively) and were not significantly less vigilant ($t = 0.64$, $d.f. = 72$, $P = 0.29$ and $t = 0.94$, $d.f. = 13$, $P = 0.43$, respectively) when the adult breeding male associated with their clan was present (Figs. 6a and 6b).

There was a male-biased sex difference in vigilance during all portions of the annual cycle. Specifically, reproductive and nonreproductive males were more vigilant and had longer lag times than females (both nursing and without litters; Figs. 3a and 3b; all $P < 0.05$ in pairwise comparisons). Reproductive and nonreproductive males had greater vigilance levels and longer lag times than females during both the breeding season and pregnancy (Figs. 3a and 3b; $P < 0.05$ for both). During lactation, both reproductive and nonreproductive males were both more vigilant and had higher lag times than nursing

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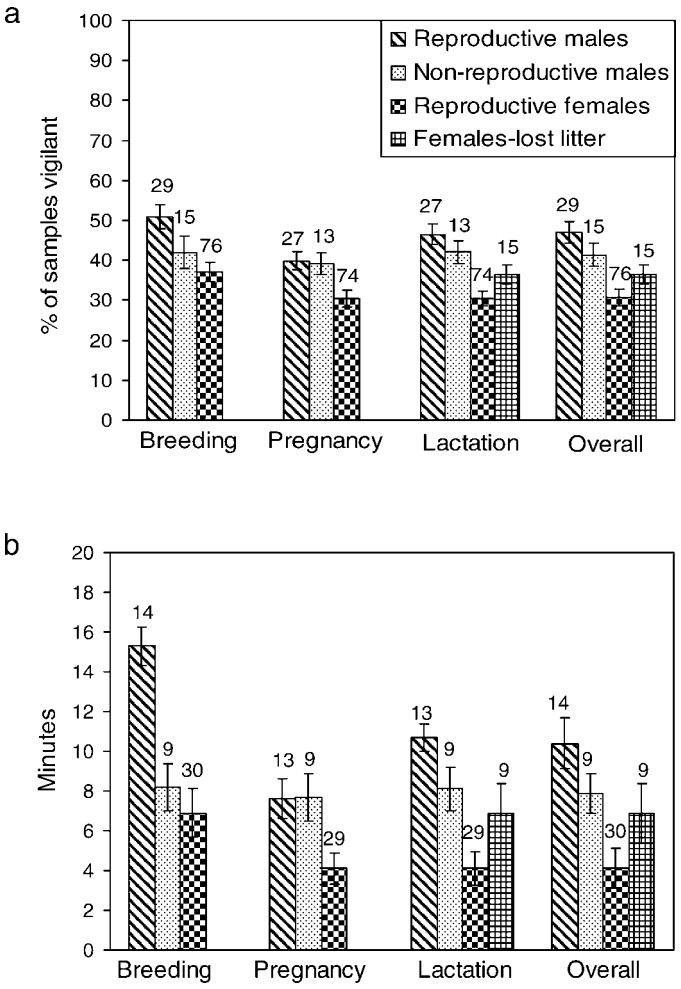


FIG. 3.—a) Percentage of samples in which subjects were vigilant and b) average lag times ± 1 *SE* for individuals that differed in sex and reproductive state over the reproductive cycle. The numbers at the top of the bars represent the number of individuals in the sample.

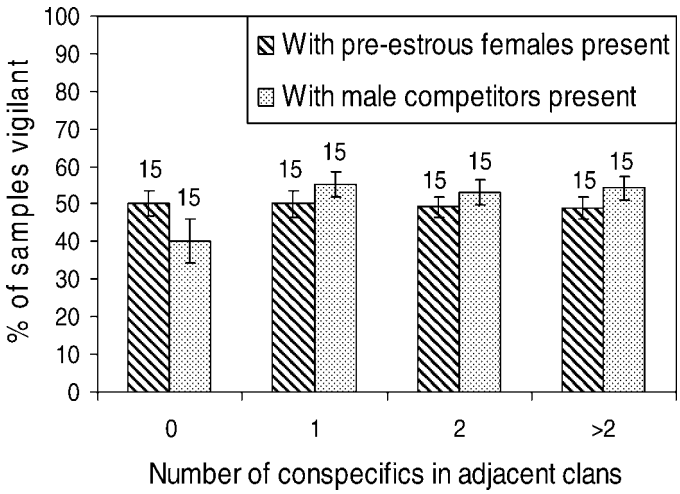


FIG. 4.—Percentage of samples in which subjects were vigilant ± 1 *SE* for reproductive males during breeding season with differing numbers of reproductive males or pre-estrous females active in adjacent clans. The numbers at the top of the bars represent the number of individuals in the sample.

females and females without litters ($P < 0.05$ for all comparisons), but reproductive males were more vigilant and had longer lag times than nonreproductive males ($t = 1.9$, $d.f. = 42$, $P < 0.05$ and $t = 2.0$, $d.f. = 21$, $P < 0.05$, respectively).

DISCUSSION

In support of the predator-detection hypothesis, the amount of time individuals allocated to vigilance decreased as the number of active conspecifics increased. As for other *Cynomys* (Hoogland 1979, 1995), this result supports the idea of larger group sizes reducing individual vigilance for predators (e.g., Elgar 1989; Hamilton 1971; Pulliam 1973; Quenette 1990) and indicates that King's (1955) predictions regarding vigilance for monitoring conspecifics do not apply to Utah prairie dogs. Furthermore, these group-size effects also occurred within family groups (clans). Individuals that have relatives watchful for predators in the clan's immediate area are likely at an advantage because predations occur in all areas of the colony (Hoogland et al. 2006). Individuals with conspecifics active in their clan can also reduce their own vigilance, regardless of whether individuals in other clans are active. This may be effective in reducing risk of predation, and also may allow individuals more time to forage (see Kildaw 1995). The predator-detection hypothesis was not supported with regard to spatial position in the colony, however, and this contrasts with results from other species (e.g., Bednekoff and Ritter 1994; Burger and Gochfield 1994; Cords 1990; Rose and Fedigan 1995).

Reproductive individuals are predicted to increase vigilance when either potential mates or competitors for mates are active. Indeed, my results indicate that reproductive individuals of both sexes were more vigilant and had longer lag times than nonreproductive individuals in these situations. That increased vigilance in estrous females serves to detect extra copulatory partners is suggested by results showing an increase in vigilance when possible mates are active from when none are active. In contrast, examination of data showing that vigilance by breeding males is not influenced by the number of pre-estrous females in adjacent clans suggests that detecting extra copulatory partners is not a primary function of vigilance for reproductive males. Instead, breeding males increase vigilance when in the presence of at least 1 other breeding male that could compete with them for territory or females.

Might the reason for increased vigilance in reproductive males be that these individuals are at a higher risk for predation? The answer here is probably no, because if the pattern were merely due to avoidance of predation, then it would be expected primarily when predation risk was higher (i.e., when the group size was smaller). Although group size and predation seemed to strongly influence vigilance, reproductive males also increased their vigilance when competitive conspecifics were active. It therefore appears that extra watchfulness results from preoccupation with competitors, which in turn may cause

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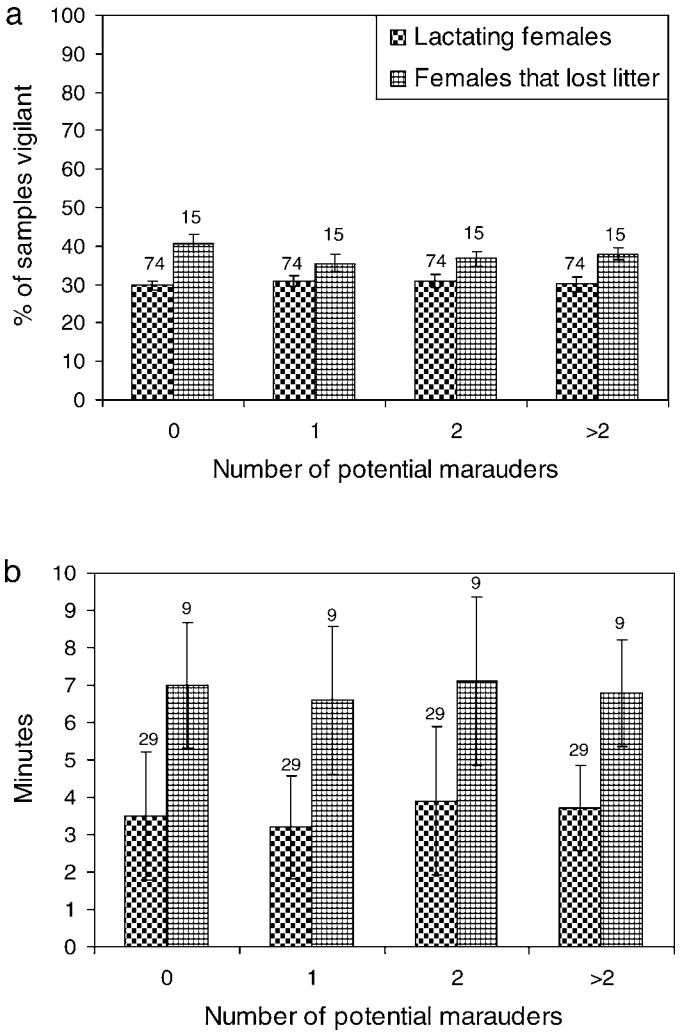


Fig. 5.—a) Percentage of samples in which subjects were vigilant and b) average lag times ± 1 *SE* for lactating females and females that lost their litter with differing numbers of potential marauders active. The numbers at the top of the bars represent the number of individuals in the sample.

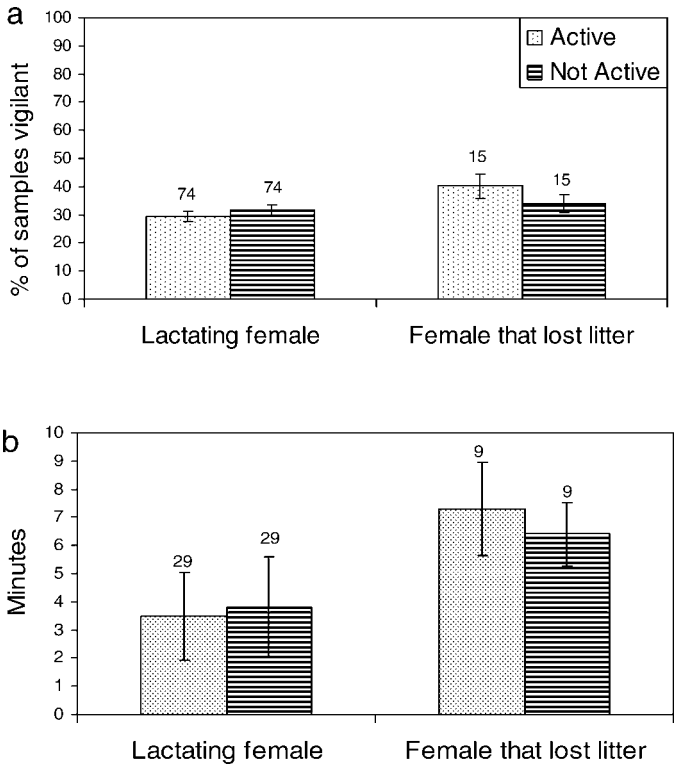


Fig. 6.—a) Percentage of samples in which subjects were vigilant and b) average lag times ± 1 *SE* for lactating females and females that lost their litter with the male associated with their clan either active or not active. The numbers at the top of the bars represent the number of individuals in the sample.

male Utah prairie dogs to be more susceptible to predation (Hoogland et al. 2006).

Defending one's offspring against infanticide should increase reproductive fitness. If females increase vigilance to protect neonates from infanticide, then nursing females should be more vigilant during lactation and in the presence of potential marauders than females that were not nursing litters. But in contrast to the infanticide-avoidance hypothesis, my results did not support these predictions. In lieu of increasing vigilance to protect neonates, might nursing females in a clan cluster around a male that has increased his vigilance to hinder infanticide by other males (McLean 1983; Steenbeek et al. 1999; Sterck et al. 1997)? The answer is probably no, as indicated by results showing that neither nursing females nor females that have lost their litters decrease their vigilance in the presence of a reproductive male clan member.

Why would nursing females not increase vigilance to protect their neonates from infanticide? There are 3 possible reasons. First, Utah prairie dogs are not as infanticidal as black-tailed prairie dogs, because fewer litters are affected and females apparently do not maraud within their clan (Hoogland 1995, 2007). Because nursing females may have greater nutritional needs (Clutton-Brock et al. 1989), perhaps we should not expect these females to be vigilant in lieu of feeding. Second, female Utah prairie dogs might be unable to prevent infanticide, because marauders are male and larger than females (Hoogland 2003), whereas in black-tailed prairie dogs, marauders are usually female and similar in size to the burrow defender. Third, perhaps nonlactating females, who were more vigilant than nursing females, may assist their close kin that are constrained by rearing their young to improve indirect fitness (Hamilton 1964) by increasing their vigilance to watch for predators or marauding conspecifics. I do not have data to investigate these intriguing possibilities.

As for black-tailed prairie dogs (Loughry 1993), males were more vigilant and had longer lag times than females over the entire reproductive cycle. Might part of the reason for increased male vigilance be that males are scanning for opportunities to commit infanticide? Alternatively, males might be more vigilant because the reproductive value of the clan is higher for males than for females, because of their limited tenure in the clan and their producing more offspring per year than individual females. If males scan for opportunities to commit infanticide, then all types of marauders (reproductive and

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nonreproductive males) should increase vigilance during lactation (i.e., when neonates are vulnerable); in contrast, only reproductive males should increase vigilance during this time if they are protecting the clan from predators or marauders. My results supported the latter prediction more closely. Although females did not seem to cluster around a male to prevent infanticide, perhaps breeding males may be extra vigilant to protect the clan from predation, because of constraints on parous females resulting from child-rearing.

Vigilance in Utah prairie dogs appears to vary mainly with the risk of predation. As a secondary function, social monitoring to increase opportunities to mate offers the best explanation for several of the patterns I found. Hwoever, associations involving vigilance and infanticide are not apparent. Perhaps future investigators will find that differences in aggression, competition, and frequency of infanticide explain why Utah prairie dogs do not increase vigilance while neonates are at risk.

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