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Author(s): John L. Hoogland, Sarah L. Hale, Ariel D. Kirk, and Yvonne D. Sui

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INDIVIDUAL VARIATION IN VIGILANCE AMONG WHITE-TAILED PRAIRIE DOGS (*CYNOMYS LEUCURUS*)

JOHN L. HOOGLAND,* SARAH L. HALE, ARIEL D. KIRK, AND YVONNE D. SUI

University of Maryland Center for Environmental Science, Appalachian Laboratory, 301 Braddock Road, Frostburg, MD 21532 (JLH)

School of Natural Resources and the Environment, The University of Arizona, Tucson, AZ 85721 (SLH)

Department of Environmental Science and Biology, State University of New York at Brockport, Brockport, NY 14420 (ADK)

Department of Biology, The University of Victoria, Victoria, BC V8W2Y2 (YDS)

**Correspondent: hoogland@al.umces.edu*

ABSTRACT—Vigilance for predators is omnipresent among species of prey. We report an investigation of vigilance of white-tailed prairie dogs (Sciuridae: *Cynomys leucurus*) living under natural conditions. Our most important conclusion concerns variation in vigilance within and among uniquely marked adult individuals ($n = 53$ in 2007, $n = 62$ in 2008). Within a single day, the percentage of observations when an individual was scanning for predators ranged from 0–100%, with a mean of 24.4%. Over a period of 3 months, some individuals were vigilant for <5% of observations, but others were vigilant for >50% of observations. For 12 of 24 individuals that we monitored for vigilance in consecutive years, levels of vigilance were significantly different between years. Some of the variation within and between individuals might have resulted from differences in vulnerability to predation.

RESUMEN—Las especies de presa constantemente se mantienen vigilantes en contra de los depredadores. Presentamos una investigación sobre la vigilancia de los perros llaneros de cola blanca (Sciuridae: *Cynomys leucurus*) que viven en condiciones naturales. Nuestra conclusión más importante se refiere a la variación en la vigilancia dentro y entre los individuos adultos marcados únicamente ($n = 53$ en el 2007, $n = 62$ en 2008). En un solo día, el porcentaje de observaciones cuando un individuo estuvo escaneado por depredadores variaron de 0–100%, con una media de 24.4%. Durante un período de 3 meses, algunos individuos se mantuvieron alerta <5% de las observaciones, pero otros estaban atentos a >50% de las observaciones. En 12 de 24 individuos a los que se ha monitoreado la vigilancia en años consecutivos, los niveles de vigilancia fueron significativamente diferentes entre años. Parte de la variación dentro y entre los individuos podría ser el resultado de diferencias en la vulnerabilidad a la depredación.

Over 140 years ago, Galton (1871) pointed out that individuals within a group sometimes can benefit from the abilities of other members of the group to detect predators and, therefore, are less likely than solitary individuals to be captured during a surprise attack. Many theoretical biologists have elaborated on this simple many-eyes effect (Pulliam, 1973; Diamond and Lazarus, 1974; Treisman, 1975a, 1975b; Caraco, 1979; Elgar, 1989; Dehn, 1990; Treves, 2000; Beauchamp, 2008), and empirical data come from a myriad of diverse species (Magurran et al., 1985; Quenette, 1990; Lima, 1995; Beauchamp, 2009; Carro and Fernandez, 2009). Furthermore, the probability that an individual within a group will itself be captured when a predator strikes is smaller than the probability for a solitary individual (Hamilton, 1971; McKaye and McKaye, 1977; Bertram, 1978; Bednekoff and Lima, 1998; Carter et al., 2009).

When awareness of predators is higher within groups because of many eyes, then individuals in groups might be able to reduce their own vigilance and consequently

have more time for foraging yet still be safer than solitary individuals from predators. In large groups, the collective amount of time devoted to vigilance can be high even though the contribution of each individual might be small (Pulliam, 1973; Quenette, 1990; Lima, 1995; Brown and Brown, 1996; Roberts, 1996; Beauchamp, 2008).

Size of the colony or group is not the only factor that affects vigilance. Other factors include competition (Samson et al., 2008; Smith and Cain, 2009), distance to safety or other conspecifics (Blumstein et al., 2001; Fernandez-Juricic et al., 2007; Unck et al., 2009), gender (Li et al., 2008; Marino and Baldi, 2008; Pays and Jarman, 2008), position within a group (Armitage, 1962; Hoogland, 1979b; Burger and Gochfield, 1994; DiBlanco and Hirsh, 2006), reproductive status (Childress and Lung, 2003; Rieucan and Martin, 2008; Monclus and Rodel, 2009), and visibility within the habitat (Marino and Baldi, 2008; Quirici et al., 2008; Bednekoff and Blumstein, 2009; Ferrari et al., 2009). Indeed, behavioral ecologists have

identified 16 factors that affect vigilance (Quenette, 1990; Lima, 1995; Treves, 2000).

The vast majority of studies of vigilance have involved unmarked individuals. Consequently, of all the factors that affect vigilance, the one for which we have the least information is probably individual variation. Only a few studies have used marked individuals, or individuals identifiable from unique natural markings, to examine variation among individuals or within the same individuals at different times, and sample sizes usually have been small (Lopez et al., 2005; Manno, 2007; Carter et al., 2009; Klose et al., 2009). We report variation in vigilance within and between marked white-tailed prairie dogs (*Cynomys leucurus*) living under natural conditions.

MATERIALS AND METHODS—White-tailed prairie dogs are large, diurnal, colonial rodents of the squirrel family (Sciuridae). On a typical day, adults (≥ 1 year old) emerge from their burrows at dawn and forage above ground until dusk. Within colonies, individuals live in territorial family groups called clans, which typically contain one sexually mature adult male, two to three sexually mature adult females, and one or two sexually immature yearling adult males (Tileston and Lechleitner, 1966; Clark, 1977; Hoogland, 1979a, 1981, 2003a). Terrestrial predators include American badgers (*Taxidea taxus*), coyotes (*Canis latrans*), and long-tailed weasels (*Mustela frenata*). Avian predators include golden eagles (*Aquila chrysaetos*) and prairie falcons (*Falco mexicanus*) (Hoogland, 1981, 2003a).

We studied a colony of white-tailed prairie dogs that occupied ca. 15 ha at the Case Ranch (latitude 40.62°, longitude -106.27°) of the Arapaho National Wildlife Refuge near Walden, Colorado. White-tailed prairie dogs at the refuge hibernated for about 5 months of each year. Males aroused from hibernation sooner than did females and started to appear above ground in late February or early March. Most females aroused from hibernation and started to appear above ground in mid-March or late March, but some females did not first appear above ground until early April (Clark, 1977; Hoogland, 1979a).

Female white-tailed prairie dogs usually attain sexual maturity and mate as yearlings in their first spring after weaning, when they weigh about 700 g. Males sometimes mate as yearlings but commonly do not attain sexual maturity and mate until they are 2 years old and weigh about 900 g (Clark, 1977; Hoogland, 2003b). Most females remain in the territory of the natal clan for life; consequently, other females of the same clan are usually kin such as mother, daughters, sisters, nieces, cousins, and so forth. Males, by contrast, usually disperse from the territory of the natal clan before mating for the first time (Hoogland, 2013).

While feeding, an adult white-tailed prairie dog commonly stands up on its hind legs and looks around. If the individual detects a predator while scanning, it usually runs to a mound at a burrow-entrance and remains vigilant and thereby visually warns nearby conspecifics of the danger. An individual sometimes also gives an alarm call after detecting a predator and thereby vocally warns conspecifics (Waring, 1970; Clark, 1977; Hoogland, 1981).

Each year, we captured, tagged, and marked every white-tailed prairie dog in a colony under study (methodological



FIG. 1—Vigilant, marked white-tailed prairie dogs (*Cynomys leucurus*) on a burrow-mound at the Arapaho National Wildlife Refuge, Colorado. Markers applied on the side with Nyanzol black dye allowed recognition of every adult at the colony each year for documentation of individual variation in vigilance.

details in Hoogland, 1995). A unique number or symbol on each individual (Fig. 1) allowed us to identify each adult and juvenile.

From 2-m high towers, we used binoculars to observe marked individuals from March–June in 2007 and 2008. In general, we and research assistants were in the towers early in the morning before the white-tailed prairie dogs first appeared above ground for the day and remained in the towers until the last individual had submerged for the night. At early and late stages of our research each year, however, we sometimes descended from our observation towers to set or check livetraps. In 2007, we recorded vigilance of white-tailed prairie dogs from 7 April–19 June. In 2008, we recorded vigilance from 17 March–10 July.

To quantify vigilance, each researcher looked for every marked adult white-tailed prairie dog in an assigned study area every 30 min. Upon detecting an individual, the researcher scored it as nonvigilant if it was on all four feet and feeding or having an interaction with another white-tailed prairie dog (e.g., fight, chase, or kiss; Clark, 1977; Hoogland, 1979a). The researcher scored the individual as vigilant if it was standing on its two hind feet and looking around or it was on a burrow-mound and either standing on its two hind feet or on all four feet (Fig. 1).

Vigilant white-tailed prairie dogs that are standing or on burrow-mounds are more conspicuous than nonvigilant, foraging individuals on all four feet amidst vegetation. We, thus, were more likely to see vigilant individuals, and, therefore, our estimates of vigilance were inflated to some unknown degree. This bias was small, however, because most individuals consistently remained near (i.e., within 100 m) our observation towers and, therefore, were easily visible whether vigilant or nonvigilant.

On cold (maximum temperature during day of $\leq 5^{\circ}\text{C}$) days in March (when hours of daylight per day were relatively few),

many white-tailed prairie dogs stayed above ground for a total of <60 min. We recorded vigilance or nonvigilance only once or twice on the same cold day for the same individual during the checks made every 30 min throughout the day. By contrast, on warm (maximum temperature during day of $\geq 20^{\circ}\text{C}$) days in June (when hours of daylight per day were many), we sometimes recorded vigilance or nonvigilance as many as 26 times on the same day for the same individual.

Over the span of 4 months each year, we scored 71% of our marked individuals as either vigilant or nonvigilant on >300 occasions, and we scored 46% of marked individuals on >600 occasions; the mean (\pm SD) number of total scorings per individual per year was 519 ± 302 . One way to examine vigilance would be to consider each single observation of vigilance as an independent data point. However, this method would unrealistically inflate the sample size. Another way to examine vigilance would be to calculate a single mean from all observations over 4 months for each individual, but this method would ignore the substantial variation that occurs within and between individuals over time and would reduce a prodigious dataset to a small number of data points. As a compromise, we used a single estimate of vigilance for each individual per day, and that daily estimate was the proportion of times that the individual was vigilant across all checks for that day. If a researcher observed an individual for 10 checks throughout a day, for example, and if the individual was vigilant for 3 of those checks, then we used a single estimate of vigilance of 30% (3/10) for the individual for that day. We considered daily estimates of vigilance from the same individual on different days to be independent. Over the 2 years, we collected 6,483 daily estimates of vigilance. For all statistical analyses, however, we only used daily estimates when we were able to record vigilance or nonvigilance a minimum of 3 times. With this restriction, we had information from 5,644 daily estimates of vigilance. The mean (\pm SD) number of recordings of vigilance or nonvigilance per individual per day for these 5,644 daily estimates was 10.10 ± 4.88 ; the cumulative number of times that we scored a white-tailed prairie dog as either vigilant or nonvigilant was $5,644 \times 10.1 = 57,123$.

Over the 2 years, we collected data from 115 adult white-tailed prairie dogs. For all 24 adults that were alive in 2007 and 2008, we collected data in both years. We did not record vigilance for juveniles. For all analyses, we used two-tailed nonparametric statistical tests.

RESULTS—In April 2007 and 2008, the numbers of adults at the colony studied were 53 and 62, respectively. In May–June 2007 and 2008, the numbers of offspring that appeared above ground from their nursery-burrows at the colony were 150 and 154, respectively. The number of recordings of vigilance or nonvigilance per white-tailed prairie dog per day ranged from 1–26 (Fig. 2) with a mean (\pm SD) of $10.10 (\pm 4.88)$ for 5,644 daily estimates of vigilance.

Four related lines of evidence indicate that white-tailed prairie dogs showed extreme variation in vigilance within and between individuals. First, the percentage of times that a white-tailed prairie dog was vigilant over the course of a day ranged from 0–100% (Fig. 3a; mean \pm SD = $24.4 \pm 21.5\%$, $n = 5,644$ daily estimates). These differences in vigilance among individuals were significant ($P < 0.001$,

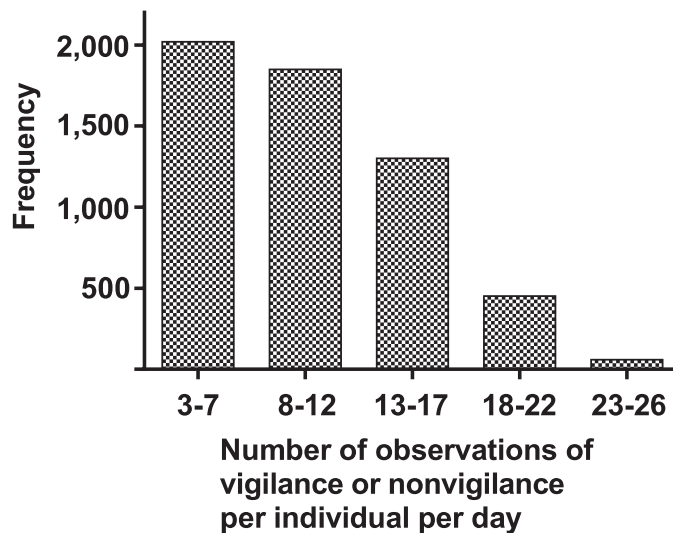


FIG. 2—Number of observations of vigilance or nonvigilance per individual per day for white-tailed prairie dogs (*Cynomys leucurus*) at the Arapaho National Wildlife Refuge, Colorado.

Kruskal-Wallis analysis of variance, $\chi^2 = 769$). For 81.5% of 5,644 daily estimates of vigilance, the percentage of times that the individual was vigilant throughout the day was <41%; for 52.2% of daily estimates, the percentage of times that the individual was vigilant throughout the day was <21%. Second, we also calculated a single overall percentage of vigilance for each white-tailed prairie dog over the entire study period. This single overall percentage for each individual was the mean of all the percentages for all the daily estimates of vigilance for that individual and showed substantial variation (Fig. 3b, $n = 105$ individuals). Third, we quantified vigilance for one representative male in 2008 and one representative female in 2008 for which we had copious information on vigilance ($n \geq 65$ daily estimates of vigilance for each; Fig. 4). The variation shown in Fig. 4 by the two individuals is typical and comparable to variation for most of the other 113 individuals that we observed in 2007 and 2008. Fourth, we also collected data on level of vigilance for 24 white-tailed prairie dogs that were alive as adults in 2007 and 2008. For 50% (12) of these individuals, levels of vigilance differed significantly between years (Table 1; $P \leq 0.050$, Mann-Whitney U test). For 37.5% (9) of the individuals that were alive in 2007 and 2008, vigilance did not differ significantly between years; for 12.5% (3) of the individuals, vigilance almost differed significantly for 2007 versus 2008 ($0.05 \leq P < 0.10$, Mann-Whitney U test).

DISCUSSION—When a white-tailed prairie dog stops feeding and stands on its hind legs or runs to a burrow-mound to scan, it presumably increases the probability that it will detect a predator or a visual alarm of a conspecific. However, an individual might scan for other reasons unrelated to predation. In particular, an individual might scan to monitor competing conspecifics (King,

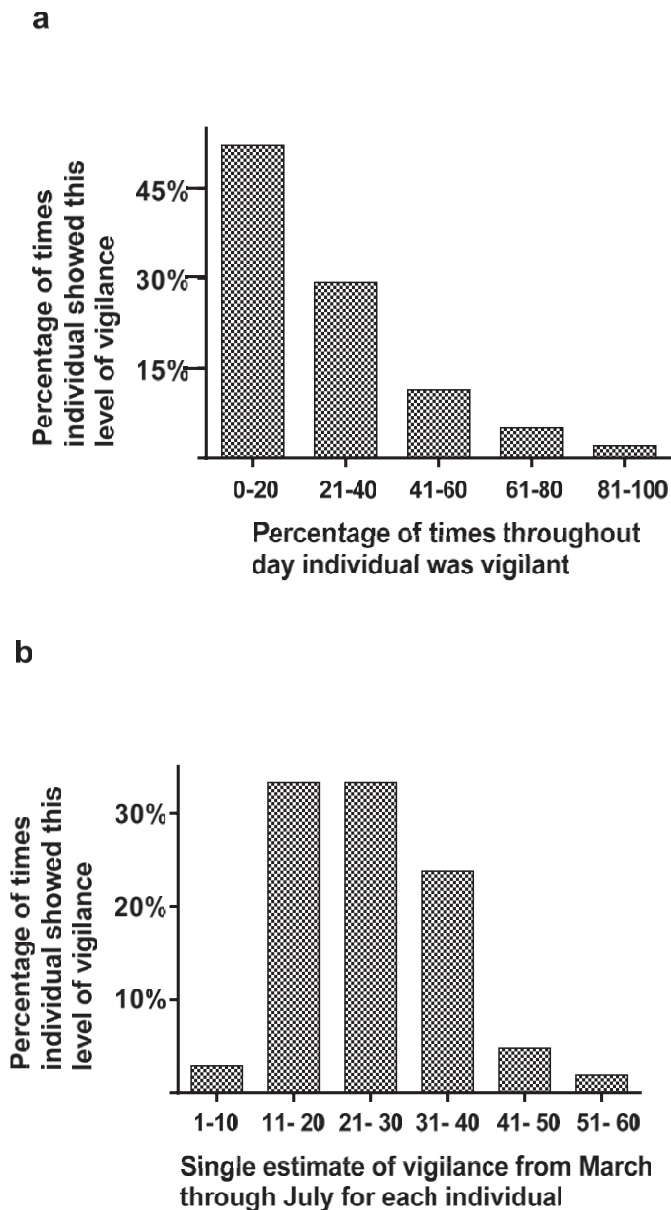


FIG. 3—**a**) Percentage of times throughout day that individual was vigilant for white-tailed prairie dogs (*Cynomys leucurus*) at the Arapaho National Wildlife Refuge, Colorado, March–July 2007 and 2008. **b**) Single estimate of vigilance for each individual white-tailed prairie dog. The single estimate was the mean of all the daily estimates for all days of observation for each individual.

1955; Treves, 1999; Blumstein et al., 2001; Manno, 2007; Macintosh and Sicotte, 2009; Favreau et al., 2010). A male might scan to watch for other males trying to invade his home territory, or a female might scan to watch for other females trying to steal nest-material from her nursery-burrow. For some colonial animals, investigators sometimes can distinguish between vigilance for competing conspecifics versus vigilance for predators, e.g., by recording whether the individual is staring directly at a nearby conspecific versus a gaze into the distance (Klose et al., 2009; Favreau et al., 2010). Due to the position of

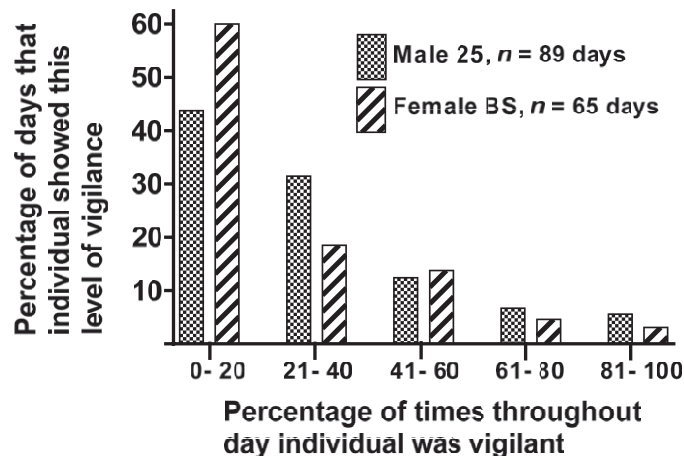


FIG. 4—Summary of vigilance of one representative male in 2008 and one representative female in 2008 for white-tailed prairie dogs (*Cynomys leucurus*) at the Arapaho National Wildlife Refuge, Colorado. These patterns are typical, and comparable variation was observed for most of the other 113 individuals studied in 2007 and 2008.

the eyes on the head of white-tailed prairie dogs, determining the object of the staring usually is not feasible. We, therefore, made no attempt to distinguish between vigilance for conspecifics versus vigilance for predators.

In almost all other studies of vigilance, investigators have not been able to identify specific individuals. By contrast, all the adults at the colony we studied ($n = 53$ in 2007, $n = 62$ in 2008) were individually marked and easily identified. Consequently, the most significant and unique feature of our research is that we have been able to measure levels of vigilance for the same individuals over time, within and between years. The variation among individuals, and for the same individual on different days or in different years, is striking.

One possible reason white-tailed prairie dogs exhibit so much variation in vigilance within and between individuals is that vigilance is simply one of many other behaviors that show substantial individual variation for animals (Krebs and Davies, 1993; Hayes and Jenkins, 1997; Lopez et al., 2005; Reale et al., 2007; Alcock, 2009; Dugatkin, 2009). A second possible reason is that individual variation in vigilance reflects real differences in vulnerability to predation (e.g., Hoogland et al., 2006) and these differences are not obvious to human observers. Perhaps, for example, certain areas within the colony we studied are especially vulnerable to a surprise attack by an American badger or a coyote, and individuals respond appropriately with a higher level of vigilance when they forage in those areas (Frid, 1997; Hunter and Skinner, 1998; Laundre et al., 2001; Li et al., 2008; Unck et al., 2009). We could not explore this possibility because we observed few unequivocal predations ($n < 5$ for 2007 and 2008) and because we did not record positions of individuals within the colony when we scored them as

TABLE 1—White-tailed prairie dogs (*Cynomys leucurus*) at the Arapaho National Wildlife Refuge, Colorado, for which vigilance differed significantly between 2007 and 2008 ($P \leq 0.05$, Mann-Whitney U test).

Prairie dog	Sex	Overall percentage of times that this individual was scanning in 2007	Overall percentage of times that this individual was scanning in 2008	Comments
C6	Female	31.9	48.3	No litter in 2007 or 2008
5-stripe	Female	37.7	12.1	Litter in 2007, no litter in 2008
F7	Female	33.6	11.1	Litter in 2007 and 2008
3SRS	Female	42.4	5.6	Litter in 2007 and 2008
C9	Female	18.8	12.5	Litter in 2007 and 2008
A4	Female	40.4	31.0	No litter in 2007, litter in 2008
B49	Female	12.4	17.4	No litter in 2007, litter in 2008
C52	Female	16.1	13.3	Litter in 2007 and 2008
D39	Female	34.1	29.6	Litter in 2007 and 2008
01	Male	35.6	18.3	Mated in 2007, did not mate in 2008
49	Male	26.0	15.6	Mated in 2007, did not mate in 2008
A13	Male	37.7	50.0	Mated in 2007 and 2008

vigilant or nonvigilant. A third possibility is that level of vigilance reflects susceptibility of specific individuals to predation (Carter et al., 2009). For example, perhaps an individual has incurred a recent injury from a fight and cannot run fast and, thus, responds with higher levels of vigilance. Similarly, as for other species (Trombulak, 1989; Trillmich et al., 2003; Hoogland, 2007), the ability to run fast to escape from predators probably varies with body mass for white-tailed prairie dogs. If so, individuals that are not at the optimal body mass for running fast (e.g., heavy just before hibernation, heavy because of late pregnancy, or of low body mass because of poor condition) might compensate via higher levels of vigilance.

Carter et al. (2009) argued that more studies of marked or individually distinctive individuals will be crucial for a better understanding of a phenomenon such as vigilance that is so ubiquitous among species that are prey. Our study of variation in vigilance within and among marked individuals of white-tailed prairie dogs is an important step in the right direction. Additional studies, especially with animals that allow researchers to discriminate between vigilance for predators versus vigilance for competing conspecifics, also will be valuable.

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LITERATURE CITED

- ALCOCK, J. 2009. Animal behavior. Sinauer, New York.
- ARMITAGE, K. B. 1962. Social behaviour of a colony of the yellow-bellied marmot (*Marmota flaviventris*). *Animal Behaviour* 10:319–331.
- BEAUCHAMP, G. 2008. What is the magnitude of the group-size effect on vigilance? *Behavioral Ecology* 19:1,361–1,368.
- BEAUCHAMP, G. 2009. How does food density influence vigilance in birds and mammals? *Animal Behaviour* 78:223–231.
- BEDNEKOFF, P. A., AND D. T. BLUMSTEIN. 2009. Peripheral obstructions influence marmot vigilance: integrating observational and experimental results. *Behavioral Ecology* 20:1,111–1,117.
- BEDNEKOFF, P. A., AND S. L. LIMA. 1998. Re-examining safety in numbers: interactions between risk dilution and collective detection upon predator targeting behaviour. *Proceedings of the Royal Society of London B* 265:2,021–2,026.
- BERTRAM, B. C. R. 1978. Living in groups: predators and prey. Pages 64–97 in *Behavioural ecology: an evolutionary approach*. First edition (J. R. Krebs and N. B. Davies, editors). Sinauer, Sunderland.
- BLUMSTEIN, D. T., J. C. DANIEL, AND I. G. MCLEAN. 2001. Yellow-footed rock-wallaby group size effects reflect a trade-off. *Ethology* 107:655–664.
- BROWN, C. R., AND M. B. BROWN. 1996. Coloniality in the cliff swallow: the effect of group size on social behavior. University of Chicago Press, Chicago, Illinois.
- BURGER, J., AND M. GOCHFELD. 1992. Effect of group size on vigilance while drinking in the coati, *Nasua narica*, in Costa Rica. *Animal Behaviour* 44:1,053–1,067.
- CARACO, T. 1979. Time budgeting and group size – theory. *Ecology* 60:611–617.
- CARRO, M. E., AND G. J. FERNANDEZ. 2009. Scanning pattern of greater rheas, *Rhea americana*: collective vigilance would increase the probability of detecting a predator. *Journal of Ethology* 27:429–436.
- CARTER, A. J., O. PAYS, AND A. W. GOLDIZEN. 2009. Individual variation in the relationship between vigilance and group size in eastern grey kangaroos. *Behavioral Ecology and Sociobiology* 64:237–245.

- CHILDRESS, M. J., AND M. A. LUNG. 2003. Predation risk, gender and the group size effect: does elk vigilance depend on the behavior of conspecifics? *Animal Behaviour* 66:389–398.
- CLARK, T. W. 1977. Ecology and ethology of the white-tailed prairie dog (*Cynomys leucurus*). Publications in Biology and Geology, Milwaukee Public Museum, Number 3:1–97.
- DEHN, M. M. 1990. Vigilance for predators – detection and dilution effects. *Behavioral Ecology and Sociobiology* 26:337–342.
- DIAMOND, S., AND J. LAZARUS. 1974. The problem of vigilance in animal life. *Brain Behavior and Evolution* 9:60–79.
- DI BLANCO, Y., AND B. T. HIRSCH. 2006. Determinants of vigilance behaviour in the ring-tailed coati (*Nasua nasua*): the importance of within-group spatial position. *Behavioral Ecology and Sociobiology* 61:173–182.
- DUGATKIN, L. A. 2009. Principles of animal behavior. Norton, New York.
- ELGAR, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews of the Cambridge Philosophical Society* 64:12–33.
- FAVREAU, F., A. W. GOLDIZEN, AND O. PAYS. 2010. Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. *Proceedings of the Royal Society of London B* 277:1–7.
- FERNANDEZ-JURICIC, E., G. BEAUCHAMP, AND B. BASTAIN. 2007. Group-size and distance-to-neighbour effects on feeding and vigilance in brown-headed cowbirds. *Animal Behaviour* 73:771–778.
- FERRARI, C., G. BOGLIANI, AND A. VON HARDENBERG. 2009. Alpine marmots (*Marmota marmota*) adjust vigilance behaviour according to environmental characteristics of their surroundings. *Ethology Ecology and Evolution* 21:355–364.
- FRID, A. 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. *Animal Behaviour* 53:799–808.
- GALTON, F. 1871. Gregariousness in cattle and men. *MacMillan's Magazine* 23:353–357.
- HAMILTON, W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31:295–311.
- HAYES, J. P., AND S. H. JENKINS. 1997. Individual variation in mammals. *Journal of Mammalogy* 78:274–293.
- HOOGLAND, J. L. 1979a. Aggression, ectoparasitism, and other possible costs of prairie dog (*Sciuridae: Cynomys* spp.) coloniality. *Behaviour* 69:1–35.
- HOOGLAND, J. L. 1979b. The effect of colony size on individual alertness of prairie dogs (*Sciuridae: Cynomys* spp.). *Animal Behaviour* 27:394–407.
- HOOGLAND, J. L. 1981. The evolution of coloniality in white-tailed and black-tailed prairie dogs (*Sciuridae: Cynomys leucurus* and *C. ludovicianus*). *Ecology* 62:252–272.
- HOOGLAND, J. L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago, Illinois.
- HOOGLAND, J. L. 2003a. Prairie dogs. Pages 232–247 in *Wild mammals of North America* (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors). Johns Hopkins University Press, Baltimore, Maryland.
- HOOGLAND, J. L. 2003b. Sexual dimorphism in five species of prairie dogs. *Journal of Mammalogy* 84:1,254–1,266.
- HOOGLAND, J. L. 2007. Alarm calling, multiple mating, and infanticide among black-tailed, Gunnison's, and Utah prairie dogs. Pages 438–452 in *Rodent societies* (J. O. Wolff and P. W. Sherman, editors). University of Chicago Press, Chicago, Illinois.
- HOOGLAND, J. L. 2013. Prairie dogs disperse when all close kin have disappeared. *Science* 339:1,205–1,207.
- HOOGLAND, J. L., K. E. CANNON, L. M. DEBARBIERI, AND T. G. MANNO. 2006. Selective predation on Utah prairie dogs. *American Naturalist* 168:546–52.
- HUNTER, T. B., AND J. D. SKINNER. 1998. Vigilance behavior in African ungulates: the role of predation pressure. *Behaviour* 135:195–211.
- KING, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairiedog town in the Black Hills of South Dakota. Contribution of the Laboratory of Vertebrate Biology, University of Michigan 67:1–123.
- KLOSE, S. M., J. A. WELBERGEN, A. W. GOLDIZEN, AND E. K. V. KALDO. 2009. Spatio-temporal vigilance architecture of an Australian flying-fox colony. *Behavioral Ecology and Sociobiology* 63:371–380.
- KREBS, J. R., AND N. B. DAVIES. 1993. An introduction to behavioural ecology. Wiley-Blackwell, New York.
- LAUNDRE, J. W., L. HERNANDEZ, AND K. A. ALTENDORF. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, USA. *Canadian Journal of Zoology* 49:1,401–1,409.
- LI, Z. Q., Z. A. JIANG, AND G. BEAUCHAMP. 2008. Vigilance in Przewalski's gazelle: effects of sex, predation risk and group size. *Journal of Zoology* 27:302–308.
- LIMA, S. L. 1995. Back to the basics of anti-predator vigilance: the group-size effect. *Animal Behaviour* 49:11–20.
- LOPEZ, P., D. HAWLENA, V. POLO, L. AMO, AND J. MARTIN. 2005. Sources of individual shy-bold variations in antipredator behaviour of male Iberian rock lizards. *Animal Behaviour* 69:1–9.
- MACINTOSH, A. J. J., AND P. SICOTTE. 2009. Vigilance in ursine black and white colobus monkeys (*Colobus vellerosus*): an examination of the effects of conspecific threat and predation. *American Journal of Primatology* 11:919–927.
- MAGURRAN, A. E., W. J. OULTON, AND T. J. PITCHER. 1985. Vigilant behavior and shoal size in minnows. *Zeitschrift fur Tierpsychologie* 67:167–178.
- MANNO, T. G. 2007. Why are Utah prairie dogs vigilant? *Journal of Mammalogy* 88:555–563.
- MARINO, A., AND R. BALDI. 2008. Vigilance patterns of territorial guanacos (*Lama guanicoe*): the role of reproductive interests and predation risk. *Ethology* 114:413–423.
- McKAYE, K. R., AND N. M. McKAYE. 1977. Communal care and kidnapping of young by parental cichlids. *Evolution* 31:674–681.
- MONCLUS, R., AND H. G. RODEL. 2009. Influence of different individual traits on vigilance behaviour in European rabbits. *Ethology* 115:758–766.
- PAYS, O., AND P. J. JARMAN. 2008. Does sex affect both individual and collective vigilance in social mammalian herbivores?: the case of the eastern grey kangaroo. *Behavioral Ecology and Sociobiology* 62:757–767.
- PULLIAM, H. R. 1973. On the advantages of flocking. *Journal of Theoretical Biology* 38:19–422.
- QUENETTE, P. Y. 1990. Functions of vigilance behavior in mammals - a review. *Acta Oecologica* 11:801–818.
- QUIRICI, V., R. A. CASTRO, J. OYARZUN, AND L. A. EBENSBERGER. 2008.

- Female degus (*Octodon degus*) monitor their environment while foraging socially. *Animal Cognition* 11:441–448.
- REALE, D., S. M. READER, D. SOL, P. T. McDOUGALL, AND N. J. DINGERMANSE. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* 82:291–318.
- RIEUCAU, G., AND J. G. A. MARTI. 2008. Many eyes or many ewes: vigilance tactics in female bighorn sheep *Ovis canadensis* vary according to their reproductive status. *Oikos* 117:501–506.
- ROBERTS, G. 1996. Why individual vigilance declines as group size increases. *Animal Behaviour* 51:1,077–1,086.
- SAMSON, A., W. CRESSWELL, J. MINDERRMAN, AND J. LIND. 2008. Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit? *Animal Behaviour* 75:869–1875.
- SMITH, S. M., AND J. W. CAIN. 2009. Foraging efficiency and vigilance behaviour of impala: the influence of herd size and neighbour density. *African Journal of Ecology* 47:109–118.
- TILESTON, J. V., AND R. R. LECHLEITNER. 1966. Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado. *American Midland Naturalist* 75:292–316.
- TREISMAN, M. 1975*a*. Predation and the evolution of gregariousness. I. Modes for concealment and evasion. *Animal Behaviour* 23:799–800.
- TREISMAN, M. 1975*b*. Predation and the evolution of gregariousness. II. An economic model for predator-prey interaction. *Animal Behaviour* 23:801–825.
- TREVES, A. 1999. Within-group vigilance in red colobus and redbellied monkeys. *American Journal of Primatology* 48:113–126.
- TREVES, A. 2000. Theory and method in studies of vigilance and aggregation. *Animal Behaviour* 60:711–722.
- TRILLMICH, F., M. BIENECK, E. GEISSLER, AND H. J. BISCHOF. 2003. Ontogeny of running performance in the wild guinea pig (*Cavia aperea*). *Mammalian Biology* 68:214–223.
- TROMBULAK, S. C. 1989. Running speed and body mass in Belding's ground squirrels. *Journal of Mammalogy* 70:194–197.
- UNCK, C. E., J. M. WATERMAN, L. VERBURGT, AND P. W. BATEMAN. 2009. Quantity versus quality: how does level of predation threat affect Cape ground squirrel vigilance? *Animal Behaviour* 78:625–632.
- WARING, G. H. 1970. Sound communications of black-tailed, white-tailed, and Gunnison's prairie dogs. *American Midland Naturalist* 83:167–185.

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