



Conspecific presence and microhabitat features influence foraging decisions across ontogeny in a facultatively social mammal

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Abstract

Natural selection is expected to favor the evolution of threat-sensitive behaviors that permit individuals to adaptively detect and respond to danger. However, because time allocated to vigilance reduces the amount of time that is available for energy acquisition, foraging in the face of predation can impose an evolutionary trade-off. Optimal foraging theory therefore predicts that risk-taking decisions should vary in response to perceived levels of threat. Our goal here is to disentangle the relative contributions of conspecific presence, ecological factors, and individual traits on two measures of vigilance in free-living California ground squirrels (*Otospermophilus beecheyi*). This facultatively social and ecologically flexible rodent represents a major source of prey in California grasslands. Over a 5-year period, we collected 386 focal animal surveys on 156 free-living individuals residing at two colony sites. Individuals were most vigilant in conditions for which predation risk was highest, such as when foraging alone and on flat areas with low vegetative cover. In general, juvenile foragers were more gregarious but less vigilant than adult foragers. Although all animals—regardless of age or sex—generally decreased their intensity of vigilance as group size increased, only adults decreased their time allocated to vigilance in response to conspecific presence. Thus, grouping consistently buffered the costs of foraging for risk-averse adults, but the benefits of conspecific presence were less salient for juveniles. Taken together, our findings highlight the importance of context in shaping foraging decisions and offer insights into the suite of factors mediating decision-making in socially and ecologically variable environments.

Significance statement

Animals face trade-offs when foraging in the face of predation, but the capacity for individuals to respond appropriately to subtle changes in context-dependent threats remains poorly understood. We studied antipredator vigilance by the California ground squirrel, a flexible species that may forage alone or in small groups of various sizes and in habitats that vary in their protective value from predators and the ease at which prey may detect predators. Although adults are more sensitive to changes in group size, all animals detected context-dependent danger to some extent. Our findings offer insights into the multiple factors that prey respond to when making foraging decisions, suggesting that animals possess the ability to integrate disparate sources of information about danger to optimize energy gain.

Keywords Dilution effect · Group-living · Ontogeny · Optimal foraging theory · Vigilance

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Introduction

Natural selection favors the evolution of threat-sensitive behaviors that permit individuals to detect and adaptively respond to danger (Dill 1987; Helfman 1989; Caro 2005). Classically defined, vigilance is any behavior that increases the likelihood that an individual will detect a stimulus (Dimond and Lazarus 1974). Antipredator vigilance permits prey to detect and avoid predators (FitzGibbon 1989; Watson

et al. 2007). Despite the survival benefits of antipredator vigilance (Boland 2003), it is nearly impossible for most animals to effectively forage and be vigilant at the same time (McNamara and Houston 1992; Kacelnik and Bateson 1996, but see: Banks et al. 2015). Allocating too much time to vigilance may reduce survival (Werner and Anholt 1993; Stamps 2007; Watson et al. 2007) and reproduction (Ruckstuhl et al. 2003; Creel et al. 2007). Prey must trade off between vigilance and other activities, such as foraging, courtship, and defense (Milinski and Heller 1978; Sih 1980; Helfman 1989; Lima and Dill 1990).

Optimal foraging theory predicts that individuals should adaptively divide their time between antipredator vigilance and foraging (Stephens and Krebs 1986; Parker and Smith 1990). This trade-off is well documented for birds (Reboreda and Fernandez 1997; Watson et al. 2007; Powolny et al. 2014) and mammals [e.g., ungulates (Ruckstuhl et al. 2003; Pays et al. 2007; Li and Jiang 2008), rodents (Arenz and Leger 2000; Fairbanks and Dobson 2007; Lea and Blumstein 2011), carnivorans (Hollén and Manser 2006; Pangle and Holekamp 2010), marsupials (Favreau et al. 2015)]. Yet, we know surprisingly little about the extent to which multiple factors simultaneously shape context-dependent foraging. That is, although foragers are likely sensitive to multiple important trade-offs at once and expected to vary in their responsiveness to changing conditions (Stephens 2008), we lack a fundamental understanding of why members of certain species, or even individuals within the same population, differentially allocate their time to vigilance (Stamps 2007). An integrative perspective is required to provide insights into context-dependent perception and management of risk by animals (Lima and Dill 1990; Caro 2005).

Social, ecological, and individual factors may interact to explain variation in vigilance. First, individuals typically take the most risks when foraging in groups (Elgar 1989; Roberts 1996; Treves 2000; Beauchamp 2008). Second, vigilance may vary with immediate ecological conditions, such as by season (Metcalf and Furness 1984; Reboreda and Fernandez 1997; Xia et al. 2011) or microhabitat features (Cowlshaw 1997; Sharpe and Van Horne 1998; Embar et al. 2011). Finally, decisions may vary with an individual's attributes, such as age (Boggs 1992; Arenz and Leger 2000; Pangle and Holekamp 2010), sex (Pays and Jarman 2008; Li et al. 2012; Whiteside et al. 2016), and/or body mass (Powolny et al. 2014; Chmura et al. 2016). Whereas some studies focus on the contributions of one or a subset of these factors, few simultaneously investigate their relative effects on vigilance within a single study and over time.

Our research aims to fill an important knowledge gap by uncovering the extent to which these factors interact to shape context-dependent, risk-sensitive behavior within a natural context. Here, we used a 5-year data set to investigate how conspecific presence, ecological factors, and

individual traits shape the trade-off between foraging and vigilance in a facultatively social rodent, the California ground squirrel (*Otospermophilus beecheyi*). This socially and ecologically flexible species offers a particularly interesting model for studying this phenomenon. It forages alone or in groups of various sizes on a range of diet items and is locally abundant across its range, representing an important prey source in California grasslands (Smith et al. 2016).

Context is the composite of biotic and abiotic variables in the local environment used by individuals to assess their immediate actions and anticipate future probabilities of events, such as impending predatory threats (Owings and Coss 1991; Ayon et al. 2017). We therefore expected conspecific presence, ecological factors, and individual traits to explain patterns of risk-taking—measured as the proportion of time allocated to vigilance and rates of vigilance during foraging—in the California ground squirrel. The former measure offers insights into opportunity costs (e.g., trade-offs between time allocated to vigilance and other behaviors) whereas the latter informs our understanding of vigilance intensity (e.g., urgency to escape, Lima and Dill 1990).

First, we expected a negative relationship between the presence of group members and vigilance. Group foraging should enhance per capita detection of predators (e.g., “many eyes effect,” Pulliam 1973) and/or reduce consumption of prey (e.g., “selfish-herd effect,” Hamilton 1971; “dilution effect,” Bertram 1978). Although social vigilance may mask or counterbalance the benefits of antipredator vigilance in highly social species (Cords 1990; Yáber and Herrera 1994; Hirsch 2002; Kutsukake 2006; Lung and Childress 2006; Favreau et al. 2010), the effects of foraging competition and social monitoring on vigilance should be limited for California ground squirrels. This species forages primarily on seeds evenly distributed across its habitat (Smith et al. 2016). Moreover, despite its maintenance of affiliative social networks in our study area (Smith et al. 2018), affiliative exchanges (e.g., nose to cheek or nose-to-nose greetings, sitting in body contact) are likely limited during foraging.

Second, we expected major features of the microhabitat—incline and vegetation height—to predict risk-sensitive behavior during foraging. With respect to incline, we examined how the steepness of the foraging substrate influenced vigilance. In general, predator detection by rodents increases with slope steepness (Blumstein et al. 2004; Embar et al. 2014; Chmura et al. 2016). We also know that, outside of the foraging context, California ground squirrels engage in most of their vigilance on elevated promontories, such as on rocks or logs; this is presumably because doing so allows for increased visual and auditory detection of predators (Leger et al. 1983). Thus, we expected California ground squirrels to allocate less time to vigilance when foraging on steep slopes. We

also predicted that vigilance should vary with a second habitat variable, vegetation height (Blumstein et al. 2004; Bednekoff and Blumstein 2009). Although there are notable exceptions (Schooley et al. 1996; Bakker 2006), most rodent species increase their vigilance in areas of low vegetation because they suffer from increased predation by mammals and raptors in open habitats (Lima and Dill 1990; Longland and Price 1991; Tchabovsky et al. 2001; Smith and Batzli 2006; Verdolin 2006; Watson et al. 2007). Importantly, California ground squirrels are also most likely to encounter their main predator, the Northern Pacific rattlesnake (*Crotalus oreganus*), in open areas (Coss 1991). We therefore expected subjects to be most vigilant when foraging in open areas with low vegetation, especially on flat surfaces.

Third, temporal variation in danger and energetic demands may predict vigilance during foraging (Lima and Bednekoff 1999). We expected animals to allocate increased time to foraging early in the summer, a time of year during which adults face increased energetic needs to recover from energy allocated to mating and reproduction (Owings and Coss 1977). Juveniles are also expected to forage intensively early in the summer following weaning. Whereas adults possess proteins in their blood to cope with venom, rattlesnake bites are lethal to juveniles of insufficient body masses (Poran et al. 1987). Within days, individuals might also vary their vigilance-foraging effort, but the expected directionality of diel variation is unclear. California ground squirrels face multiple threats from predators throughout the day (Smith et al. 2016).

Finally, individual traits may also affect foraging decisions. First, in multiple species, juveniles are less vigilant than adults (Loughry and McDonough 1989; Arenz and Leger 2000; Bednekoff and Blumstein 2009; Beauchamp 2015). Experiments on California ground squirrels suggest that juveniles are also less reactive than adults to predator stimuli (Putman et al. 2015). Thus, we expected juveniles to be less vigilant than adults when foraging in natural conditions. Second, although an individual's sex might influence its risk sensitivity, sex-biased vigilance may vary by season or context (Reboreda and Fernandez 1997; Pays and Jarman 2008; Powolny et al. 2014). In California ground squirrels, although parous females are more responsive to alarm calls than non-parous adult females (Leger and Owings 1978), we expected minimal sex differences in our current study. Because our goal was to study vigilance across ontogeny, we conducted observations annually at a time of year after which young of the year were weaned and adults were no longer reproducing. Finally, body condition may influence risk-taking. After controlling for day of the year, we expected the heaviest animals (in the best condition) to be most vigilant, although these effects may vary with age (Bachman 1993; Chmura et al. 2016).

Methods

Study site and subjects

From 2013 to 2017, we studied free-living California ground squirrels at Briones Regional Park in Contra Costa County, CA, USA (latitude 37.9377014 North, longitude 122.1388542 West, elevation 319 m above mean sea level). We monitored subjects from early May to late July, a time of year during which juveniles (young of the year) and adults are most active aboveground (Holekamp and Nunes 1989). The study site consists primarily of open oak savannah interspersed with vegetated riparian corridors. Subjects resided at two distinct colony sites located to the west of Alhambra Creek Staging Area that vary in their degree of human disturbance and level of vegetation management (Fig. 1). The first colony (Crow, ~9596 m²) resides in an old walnut grove with moderate foot traffic and modest mowing (typically only once at the start of the summer field season). The second colony (Paradise, ~9540 m²) is subject to limited seasonal grazing by domestic cattle (ending by the start of the summer), but no mowing and only rare disturbances by humans. The major natural predators are rattlesnakes, coyotes (*Canis latrans*), red-tailed hawks (*Buteo jamaicensis*), and Peregrine falcons (*Falco peregrinus*). Domestic dogs (*C. lupus familiaris*) regularly visit both areas, but disturbances by off-leash dogs are most common in Crow.

Live-trapping of free-living animals

We live-trapped and released California ground squirrels using Tomahawk Live Traps (Hazlehurst, WI, USA) baited with black oil sunflower seeds and peanut butter on a biweekly schedule at the two colony sites (for details, see Smith et al. 2018). Using a cone-shaped handling bag (Koprowski 2002), we recorded each subject's mass, sex, and reproductive status. Upon first capture, we marked each subject with a Monel ear tag and a passive integrated transponder (PIT) tag (Biomark Inc., Idaho, NE, USA). For visual identification, we also gave them a unique fur mark with Nyanzol cattle dye (Greenville Colorants, NJ, USA). Juveniles were weaned young of the year (60 to 365 days of age) whereas adults were older than 365 days (Hanson and Coss 1997). We assigned marked individuals to age categories with high accuracy (Smith et al. 2018). Our data also include repeated measures, permitting us to track vigilance patterns for some individuals across contexts and between age categories.

Behavioral observations

From 0800 to 1300 h, we conducted behavioral observations on most weekdays during which no trapping occurred and trained observers easily recognized subjects from a distance



Fig. 1 Satellite map of the study area showing the two colony sites: Paradise (west) and Crow (east). White lines represent colony boundaries at Briones Regional Park in Contra Costa County in the Bay Area of California. Whereas Paradise (~9540 m²) is subject to limited seasonal

grazing by domestic cattle (ending by the start of the summer), no mowing, and only rare disturbances by humans, the Crow colony resides in an old walnut grove in an area (~9596 m²) subject to moderate foot traffic and mowing at the start of the summer field season

(for details, see Smith et al. 2018). Behavioral observations totaled 769 h over 159 observation days in the summers of 2013 to 2017. Briefly, trained observers watched animals from one of several set locations within each colony site (e.g., picnic table or lawn chair) and sat at a distance (> 20 m) to avoid influencing behavior (Smith et al. 2018). On average, observers waited $124 \pm \text{SE } 4$ min ($N = 386$ surveys) after the start of their observation session before starting focal animal surveys. This limited disturbance to subjects and ensured habituation to observers. For the current study, we selected foraging subjects for focal animal surveys using a regular sampling regime and according to a fixed schedule to increase the evenness of sampling across subjects (Altmann 1974). This approach also limited the sampling of multiple individuals from the same group within an observation session. In total, we collected 240 surveys on individuals foraging alone. For those collected on individuals foraging in groups ($N = 146$ surveys), we sampled an average of $1.01 \pm \text{SE } 0.01$ individuals from each group. For individuals sampled more than once within a summer, on average, $10 \pm \text{SE } 1$ days ($N = 77$ individuals) elapsed between consecutive surveys. It was not possible to record data blind because our study involved focal animals in the field.

Surveys were conducted in the late mornings and early afternoons, a period after which most socializing (e.g., playing, greeting; Smith et al. 2018) ended, to capture peaks in foraging behavior in this diurnal species (Owings et al.

1977). Prior to starting each survey, the recorder noted the colony site, date, time of day, and identity of the subject as well as group size and ecological variables. Because vigilance by California ground squirrels is most sensitive to environmental changes within 5 m (Leger et al. 1983), here we considered conspecifics to be present when they were within 5 m of the focal animal. Following Owings et al. (1977), we categorized vegetation height as high when it effectively covered the body of adult subjects engaged in quadrupedal foraging and low when it did not; defined this way low vegetation was less than 10 cm (including dirt patches lacking vegetation) and high vegetation was greater than or equal to 10 cm. Finally, following Blumstein et al. (2004), we recorded the incline of the foraging substrate relative to the ground to describe the steepness of the foraging terrain. Slope of the foraging animal was recorded based on the angle of an animal's substrate relative to the horizon. Formally, this was calculated as $\tan^{-1}(y/x)$ where x is the horizontal run of the horizon and y is the vertical rise of the substrate. In practice, trained observers accurately distinguished between foragers on low (angle less than 10°) and high (angle greater than or equal to 10°) inclines from a distance without disturbing subjects.

Following Lea and Blumstein (2011), we established an ethogram to measure the frequency and duration of all behaviors by California ground squirrels within the context of foraging (for details, see: Smith et al. 2016). Briefly, "foraging" animals assumed a quadrupedal posture (stand forage:

standing on all fours with head down, pointing nose towards the ground, and chewing) or a bipedal posture (rear forage: standing upright on hind limbs, pointing nose towards the food item, and chewing). “Vigilance” included looking while in a quadrupedal posture (stand look: while on all fours, head is off the ground, and pointed in a direction of interest) or bipedal posture (rear look: while on hind limbs, head is away from substrate, and pointing towards a direction of interest). Importantly, we scored a “look” for each instance a focal animal stopped chewing or collecting seed to scan the horizon; we calculated rates of vigilance based on these looks. Terrestrial locomotion was categorized as “walking” (at least two paws were on the ground at a time) or “running” (gait included an aerial phase—all four paws off the ground at once). All behaviors not explicitly in this foraging ethogram were scored as “other.” We limited analyses to times when focal individuals were in visual range.

In the field, observers recorded focal animal surveys into digital voice recorders. Surveys ($N = 386$) lasted an average of $3.0 \pm \text{SE } 0.1$ min. This short sampling period captured individuals foraging within a single group size and ecological context (as done elsewhere; e.g., Lea and Blumstein 2011; Chmura et al. 2016). We ended a survey if a subject was out of sight for > 1 min. In the lab, two independent scorers quantified audio recordings using JWatcher 1.0 software (Blumstein and Daniel 2007). Interobserver reliability refers to the accuracy of scoring each audio recording, which in each case exceeded 95%.

Statistical analyses

We used R version 3.5.1 (R Development Core Team 2018) to perform statistical analyses and made our graphs in ggplot2. First, we documented the expected trade-off between time allocated to foraging and vigilance by fitting a linear mixed effect model (LMM) with a Gaussian distribution in lme4 on the arcsine transformed data. Second, we fit a LMM with a Poisson distribution to examine the effects of life stage and sex, as well as their two-way interaction, on an individual’s average group size during foraging (Bates et al. 2014). For both LMMs, we included the random effect of identity to account for repeated measures.

To examine the factors predicting risk-taking, we fit additional LMMs with Gaussian distributions to explain each measure of vigilance—proportion of time allocated to foraging and rates of vigilance. For each measure, we ran separate models to examine the influence of grouping measured two ways—as conspecific presence (binary variable, 0 = absent, 1 = present) or as foraging group size (continuous variable, 1 to 6 individuals in group). We assessed the two group size effects on each vigilance measure to generate a total of four separate mixed effect models. We elected to first examine the binary effect of

conspecific presence on vigilance because roughly half (62.2%) of our subjects foraged alone, and most of those who foraged socially did so accompanied by only one companion (for details, see “Results”). We also tested for the effect of group size per se on vigilance because most theoretical models, derived from observations on gregarious animals foraging in large herds or flocks, base their predictions on group size measured as a continuous variable. To test for the effects of daily (within days) and seasonal (across days within a summer) variation on vigilance, we included hour of the day and day of the year, respectively, in each model. We therefore entered the fixed effects of hour, day, age category (juvenile/adult), sex (male/female), social context (as either conspecific presence (present/absent) or group size (number of conspecifics within 5 m)), vegetation height (low/high), and incline (low/high) in each of the four models examining context-dependent vigilance.

We tested for all two-way interactions between fixed effects. We retained statistically significant two-way interactions in the final models and report non-significant ones based on their sequential addition to and removal from each final model. Because the effects of age-category and mass were highly correlated ($R \geq 0.81$; i.e., masses of adults always exceeded those of juveniles), we first examined the effects of age category as a predictor variable in explaining variation for all individuals and then ran separate models to examine the effects of mass within each age category. No terms in our final models were highly intercorrelated ($R < 0.25$ for all terms). The random effects of year, colony, and squirrel identity were also included in each model to account for repeated observations of the same individuals across the study as well as potential differences among years and between colonies. We used likelihood ratio tests (LRTs) to assess whether random effects improved each model’s fit. We also conducted a two-way chi-square test to examine colony-level differences in microhabitat features of the two colonies.

The dependent variables of mean group sizes (as a function of age and sex) and rates of vigilance (as function of multiple independent variables) were consistent with model distributions and homoscedasticity of variances; we modeled these factors without transforming the data. We transformed the proportion of time allocated to vigilance data using the arcsine transformation prior to running models because this measure failed to conform to assumptions. Statistical differences were considered significant when $a \leq 0.05$.

Data availability

Datasets generated and analyzed for the current study are available from the corresponding author on reasonable request.

Results

Trade-off between foraging and vigilance

Overall, we collected 386 focal animal surveys on a total of 156 California ground squirrels observed foraging at two different colony sites over a 5-year period. In general, foragers allocated more time to acquiring energy than to other behaviors (Fig. 2). Subjects also tended to assume quadrupedal postures (while foraging or looking) more often than bipedal postures (Fig. 2). Only a small proportion of time was allocated to locomotion or socializing (included in “other”) during foraging (Fig. 2). As predicted, we detected a negative relationship between time allocated to foraging and vigilance when using an LMM to account for repeated measures (estimate $-0.671 \pm \text{SE } 0.025$, $P < 0.00001$; $N = 386$ focal animal surveys). This finding confirms the expected trade-off between foraging and vigilance for this species.

Most animals forage alone, but juveniles are moreregarious than adults

In general, foragers were most often observed by themselves (foraging group size of 1). Specifically, 62.2% of surveys were on lone individuals. Individuals foraging with at least one conspecific did so in groups comprised of 2 (23.3%), 3 (9.1%), 4 (3.6%), 5 (1.5%), or 6 (0.3%) individuals.

Foraging group size varied between age categories. On average, the foraging groups of focal juveniles (mean $\pm \text{SE } 1.7 \pm 0.1$, range of sizes: 1 to 5 individuals, $N = 72$ individuals) were significantly larger than those of focal adults (mean $\pm \text{SE } 1.4 \pm 0.1$, range of sizes: 1 to 6 individuals, $N = 97$ individuals; LMM age category 0.203 ± 0.098 , $t = 2.073$, $P = 0.040$). Neither the main effect of sex (0.074 ± 0.108 , $t = 0.682$, $P = 0.496$) nor its interaction with age category (age \times sex $P = 0.739$) significantly predicted group size; males ($N = 65$) and females ($N = 92$) foraged in groups of 1.6 ± 0.1 and 1.5 ± 0.1 , respectively. Identity did not explain a significant amount of variation in foraging group size (χ^2 ; 1.6, $df = 1$, $P = 0.201$).

Adults reduced time allocated to vigilance when foraging with conspecifics

The effect of conspecific presence on the proportion of time individuals allocated to vigilance varied significantly with the age category of the subject (LMM; age \times conspecifics $P = 0.021$, Table 1A, Fig. 3A). Overall, juveniles and adults allocated similar amounts of their time to vigilance when foraging with conspecifics ($0.037 \pm \text{SE } 0.038$, $P = 0.331$), but adults allocated significantly more time to vigilance than juveniles when foraging alone (-0.073 ± 0.032 , $P = 0.022$, Fig. 3A). Whereas adults significantly reduced their time allocated to vigilance when foraging with conspecifics (-0.106 ± 0.0388 , $P = 0.007$), time allocated by juveniles to vigilance

Fig. 2 The mean $\pm \text{SE}$ proportion of time California ground squirrels allocated to foraging while standing on all four paws (quadrupedal, stand forage) or rearing up (bipedal, rear forage), vigilance while standing on all four paws (quadrupedal, stand look) or rearing up (bipedal, rear look), locomotion (walking or running), and other activities (not included in ethogram). Data reflect 386 focal animal surveys collected on 156 unique individuals across two colonies and 5 years

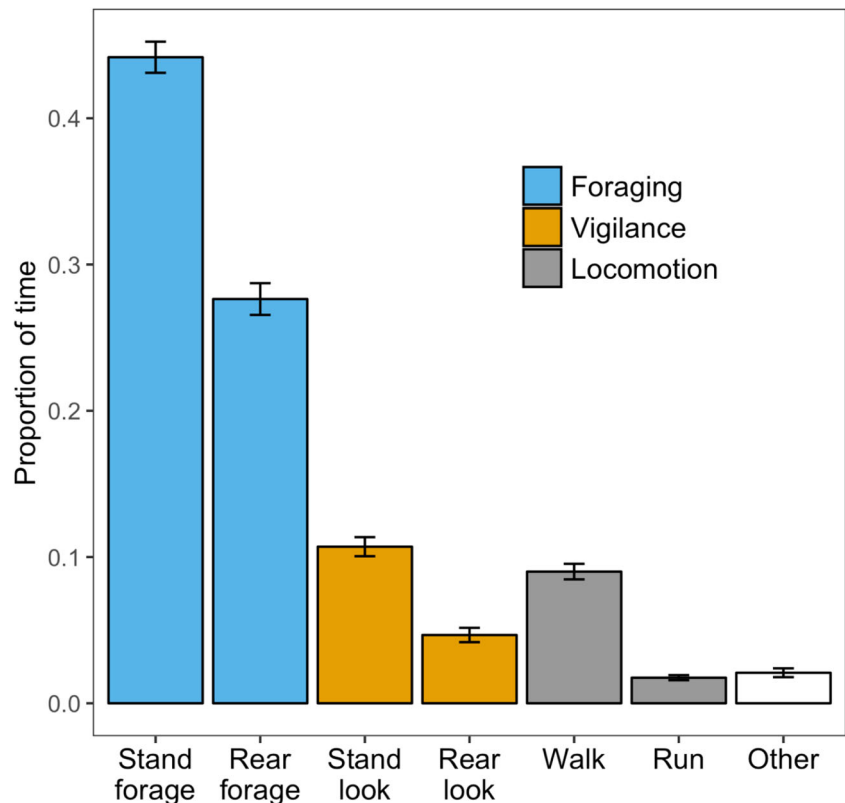


Table 1 Factors explaining proportion of time California ground squirrels allocated to vigilance

	Estimate \pm SE	<i>t</i> -value	<i>P</i> -value
A. Effects of conspecific presence (modeled as a binary variable)			
(Intercept)	0.211 \pm 0.152	1.393	0.164
Sex (female)	0.002 \pm 0.025	0.061	0.951
Hour of day	-0.004 \pm 0.008	-0.460	0.646
Angle (low)	-0.070 \pm 0.044	-1.606	0.109
<i>Day of year</i>	<i>0.001 \pm 0.001</i>	<i>2.108</i>	<i>0.036</i>
<i>Cover (low)</i>	<i>-0.076 \pm 0.029</i>	<i>-2.588</i>	<i>0.010</i>
<i>Age category (adult)</i>	<i>-0.066 \pm 0.029</i>	<i>-2.253</i>	<i>0.025</i>
<i>Conspecifics (present)</i>	<i>-0.109 \pm 0.034</i>	<i>-3.198</i>	<i>0.002</i>
<i>Age category \times conspecifics</i>	<i>0.107 \pm 0.046</i>	<i>2.314</i>	<i>0.021</i>
B. Effects of group size (modeled as a continuous variable)			
(Intercept)	0.273 \pm 0.155	1.756	0.080
Sex (female)	0.002 \pm 0.025	0.062	0.951
Hour of day	-0.004 \pm 0.008	-0.541	0.589
Angle (low)	-0.070 \pm 0.044	-1.614	0.107
<i>Day of year</i>	<i>0.001 \pm 0.001</i>	<i>2.111</i>	<i>0.035</i>
<i>Cover (low)</i>	<i>-0.077 \pm 0.029</i>	<i>-2.613</i>	<i>0.009</i>
<i>Age category (adult)</i>	<i>-0.114 \pm 0.045</i>	<i>-2.567</i>	<i>0.011</i>
<i>Group size</i>	<i>-0.059 \pm 0.017</i>	<i>-3.529</i>	<i>0.001</i>
<i>Age category \times group size</i>	<i>0.052 \pm 0.024</i>	<i>2.223</i>	<i>0.027</i>

(A) Random effects (year $\chi^2 < 0.0001$, $df=1$, $P=1.000$; colony $\chi^2 < 0.0001$, $df=1$, $P=1.000$; identity $\chi^2 = 0.212$, $df=1$, $P=0.645$) were non-significant. (B) Random effects (year $\chi^2 = 2.318$, $df=1$, $P=0.128$; colony $\chi^2 = 2.263$, $df=1$, $P=0.133$; identity $\chi^2 = 2.344$, $df=1$, $P=0.126$) were non-significant. Significant effects for (A) and (B) are in italics

was not predicted by conspecific presence (-0.001 ± 0.026 , $P=0.906$, Fig. 3A). The effects of conspecifics presence on time allocated to vigilance was consistent for both sexes (sex 0.002 ± 0.025 , $P=0.951$; sex \times conspecifics 0.017 ± 0.051 , $P=0.743$, Table 1A). Within age categories, mass failed to explain the remaining variation in the proportion of time allocated to vigilance by juveniles (-0.001 ± 0.001 , $P=0.537$) or adults (-0.001 ± 0.001 , $P=0.900$).

We further investigated these effects by entering group size as a continuous predictor variable into a second model predicting time allocated to vigilance (Table 1B). After controlling for relevant covariates, we again found a significant interaction between group size and age category on the proportion of time allocated to vigilance ($P=0.027$, Table 1B). As before (Fig. 3A), the negative relationship between group size and the proportion of time allocated to vigilance was statistically significant for adults (-0.058 ± 0.019 , $P=0.003$) but not for juveniles (-0.009 ± 0.014 , $P=0.525$, Fig. 3B); mass again failed to explain additional variation in the time allocated by juveniles (-0.001 ± 0.001 , $P=0.537$) or adults (-0.001 ± 0.001 , $P=0.987$) to vigilance. Neither the main effect of sex (Table 1B), nor its interaction with group

size (sex \times group size -0.008 ± 0.026 , $P=0.761$), explained time allocated to vigilance. Moreover, the random effect of identity failed to improve any of the four models (Tables 1 and 2).

Lowest rates of vigilance when foraging in groups

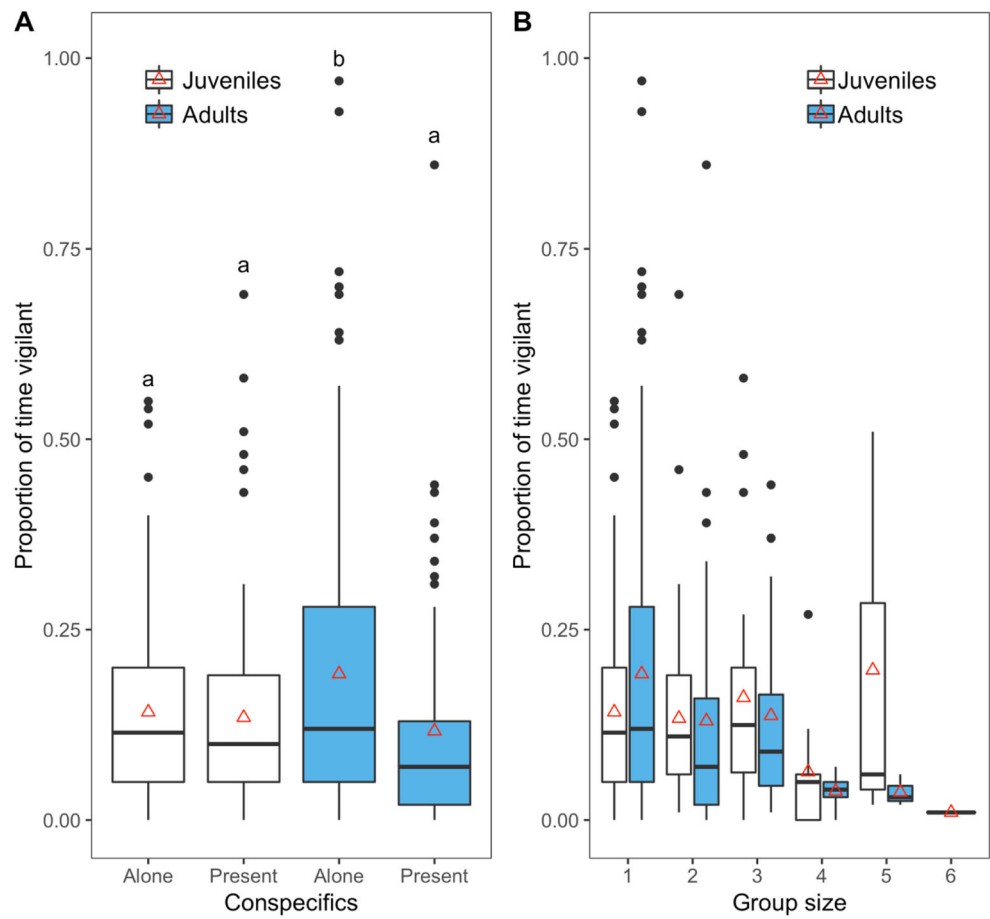
The effect of conspecific presence on rates of vigilance was consistent between age (age \times conspecifics 0.612 ± 0.640 , $P=0.340$) and sex categories (sex \times conspecifics -0.014 ± 0.651 , $P=0.983$). That is, regardless of age or sex (Table 2A), individuals scanned the environment significantly less often when foraging with conspecifics than when alone ($P=0.002$, Table 2A, Fig. 4A). These patterns remained when we modeled group size as a continuous variable; individuals significantly decreased vigilance rates as group sizes increased ($P=0.002$, Table 2B, Fig. 4B) regardless of their age (age \times group size 0.301 ± 0.327 , $P=0.359$) or sex (sex \times group size 0.037 ± 0.350 , $P=0.916$). As before, neither age nor sex predicted vigilance rates (Table 2B). Mass failed to predict vigilance rates for juveniles (-0.001 ± 0.003 , $P=0.962$; -0.001 ± 0.001 , $P=0.991$) or adults (-0.001 ± 0.002 , $P=0.704$; -0.001 ± 0.001 , $P=0.576$) regardless of whether the effects were modeled for conspecific presence and group size, respectively.

Low inclines and low vegetation promote vigilance

Animals were generally most vigilant when foraging in low vegetation and on low inclines. The increased proportion of time allocated to vigilance in low vegetation was statistically significant regardless of the group size variable in the model ($P \leq 0.010$, Table 1, Fig. 5A), but the increased rate of vigilance in low vegetation was not statistically significant (Table 2, Fig. 5B). On average, animals foraging on low (flat) inclines also tended to be more vigilant than those animals foraging on high (steep) inclines (Fig. 5). The effect of incline on the proportion of time allocated to vigilance failed to reach statistical significance regardless of how the group effect was modeled ($P=0.109$, Table 1A; $P=0.107$, Table 1B, Fig. 5A). However, for models including either group size variable, rates of vigilance were significantly higher when individuals foraged on low versus high inclines ($P \leq 0.009$, Table 2, Fig. 5B). The effects of microhabitat features on ground squirrel vigilance were additive, with no significant interactions between their effects on the proportion of time vigilant (angle \times vegetation height 0.094 ± 0.083 and -0.089 ± 0.082 , $P \geq 0.278$) or rates of vigilance (-0.289 and -0.150 ± 1.136 , $P \geq 0.895$, Fig. 5).

In general, animals surveyed in Crow ($N=335$) allocated a greater proportion of time to vigilance (mean \pm SE 0.16 ± 0.01) and displayed higher rates of vigilance (3.7 ± 0.2 looks per minute) than those sampled in Paradise (0.13 ± 0.02 of

Fig. 3 The effect of (A) conspecific presence and (B) group size on the proportion of time allocated to vigilance by foraging juvenile (white) and adult (blue) California ground squirrels. The middle quartile (dark line) represents the median; the box edges are the upper and lower quartiles; the whiskers are 50% from the median, and the closed circles correspond to the outliers, calculated as the values smaller or larger than 1.5 times the box length (i.e., upper—lower quartile). Red triangles represent means. In panel (A), different lowercase letters above boxes represent statistical differences between categories. In panel (B), the group size effect was statistically significant for adults but not juveniles



time; 2.9 ± 0.3 looks per minute; $N = 51$). Although the random effect of colony failed to explain a significant amount of additional variation for either variable beyond those explained by the main effects (Tables 1 and 2), microhabitat use significantly varied between colonies (chi-square test $\chi^2 = 256.3$, $df = 3$, $P < 0.0001$). In Crow and Paradise, respectively, foragers were sampled in the following: (i) low incline/low vegetation ($N = 287$, 7), (ii) low incline/high vegetation ($N = 50$, 6), (iii) high incline/low vegetation ($N = 0$, 13), and (iv) high incline/high vegetation ($N = 1$, 22).

Temporal patterning of vigilance

Subjects allocated significantly more time to vigilance towards the end than towards the beginning of summer regardless of how grouping factors were modeled ($P \leq 0.036$, Table 1), but sampling day failed to predict vigilance rates (Table 2). Sampling hour within days failed to predict the proportion of time subjects allocated to foraging (Table 1) or rates of vigilance (Table 2). This was the case regardless of whether hour was modeled as a linear or non-linear function. For brevity, we only report the non-significant results of the linear function for our four models (Tables 1 and 2). The effects of hour on the proportion of time allocated to vigilance

(hour \times day -0.001 ± 0.001 and -0.001 ± 0.001 , $P \geq 0.524$) or rates of vigilance (hour \times day -0.006 ± 0.007 and -0.006 ± 0.007 , $P \geq 0.422$) were additive. Data were consistent across years; the random effect of year was non-significant in our models (Tables 1 and 2).

Discussion

Our integrative approach reveals that California ground squirrels face context-dependent trade-offs between time allocated to foraging and vigilance. Interestingly, our two measures of vigilance captured unique aspects of this trade-off, highlighting the value of measuring multiple aspects of vigilance within a single study. Overall, age category—but not sex or identity—was a major contributing factor with respect to foraging in this species but the effect of ontogeny varied between the two measures of vigilance. First, juveniles typically foraged with conspecifics more often than did adults regardless of their sex. Second, when foraging alone, adults allocated significantly more time to vigilance than juveniles. Third, adults—but not juveniles—reduced the proportion of time allocated to vigilance when conspecifics were present. Fourth, we found no ontogenetic difference in how animals

Table 2 Factors explaining the rates of vigilance by foraging California ground squirrels

	Estimate ± SE	t-value	P-value
A. Effects of conspecific presence (modeled as a binary variable)			
(Intercept)	2.361 ± 2.143	1.102	0.271
Sex (female)	−0.092 ± 0.337	−0.272	0.786
Hour of day	−0.007 ± 0.110	−0.060	0.952
Angle (low)	<i>−1.596 ± 0.603</i>	<i>−2.646</i>	<i>0.009</i>
Day of year	0.010 ± 0.010	1.003	0.317
Cover (low)	−0.567 ± 0.405	−1.400	0.162
Age category (adult)	0.266 ± 0.330	0.808	0.420
<i>Conspecifics (present)</i>	<i>−1.014 ± 0.320</i>	<i>−3.168</i>	<i>0.002</i>
B. Effects of group size (modeled as a continuous variable)			
(Intercept)	3.073 ± 2.156	1.426	0.155
Sex (female)	−0.135 ± 0.337	−0.402	0.688
Hour of day	−0.011 ± 0.110	−0.102	0.919
Angle (low)	<i>−1.611 ± 0.603</i>	<i>−2.670</i>	<i>0.008</i>
Day of year	0.009 ± 0.010	0.969	0.333
Cover (low)	−0.556 ± 0.406	−1.370	0.172
Age category (adult)	0.222 ± 0.327	0.678	0.498
<i>Group size</i>	<i>−0.505 ± 0.165</i>	<i>−3.069</i>	<i>0.002</i>

(A) Random effects (year $\chi^2 = 0.610$, $df = 1$, $P = 0.435$; colony $\chi^2 < 0.001$, $df = 1$, $P = 1.000$; identity $\chi^2 < 0.001$, $df = 1$, $P = 1.000$) were non-significant. (B) Random effects (year $\chi^2 = 0.297$, $df = 1$, $P = 0.586$; colony $\chi^2 < 0.001$, $df = 1$, $P = 1.000$; identity $\chi^2 < 0.001$, $df = 1$, $P = 1.000$) were non-significant. Significant effects for (A) and (B) are in italics

varied their rates of vigilance, a measure of urgency to escape from danger, in response to conspecific presence. That is, animals of all ages reduced their intensity of vigilance as group size increased. The local ecology also shaped foraging patterns, as reflected by changes in risk-sensitive behaviors based on microhabitat use and time of the year. Specifically, animals belonging to all age-sex categories decreased vigilance in areas with high vegetation, on the steepest inclines, and early in the summer. The effects of ontogeny, group size, and microhabitat features were consistent across years, between colonies and among individuals, suggesting their salience on risk-taking by California ground squirrels.

Risk-sensitive foraging varies with group size and across ontogeny

Our results are largely consistent with the expected “group-size” effect. Indeed, group cohesion buffers the costs of (time allocated to) vigilance in the California ground squirrel. Beyond this, these data offer insights into what these animals might be looking for during foraging. Because vigilance decreased with increasing group size, our findings are consistent with previous studies indicating these prey animals are most likely scanning for predators rather than for competitors.

Only adults benefited from decreasing their proportion of time allocated to vigilance when foraging in groups of two or more individuals, suggesting that the proportion of time juveniles allocate to foraging is consistent regardless of group size. Documenting how responses to group size vary across ontogeny importantly extends our knowledge of risk-taking in this species. Previous studies suggest adults are most responsive to alarm calls (Loughry and McDonough 1989), best able to distinguish among predator types (Hanson and Coss 1997) and respond most appropriately to predators (Putman et al. 2015). Interestingly, Hanson and Coss (2001) found that, when traveling outside of their colony area to artificial feeding stations, adults ($N = 9$) were *less* vigilant than juveniles ($N = 14$); adults quickly filled their cheek pouches prior to returning to their home areas to process food. Notably, adults ($N = 97$) in our current study were *more* vigilant than juveniles ($N = 72$), suggesting we captured important ontogenetic variation under naturalistic conditions but that strategies vary with the nutritional value of forage.

One possible explanation for the ontogenetic differences documented here is that juveniles simply lack the social or cognitive skills required to perceive and/or adaptively respond to changes in their foraging group. Indeed, adaptive foraging decisions rely upon an individual’s ability to accurately estimate and adjust to relevant environmental information (Dall et al. 2005). In many species, young animals are less informed about threats than are adults (Beauchamp 2018). Although future studies are required to rule out this possibility, our finding that juveniles—like adults—adaptively modified rates of vigilance in response to foraging group size suggests juveniles are not socially naïve. Instead, increased selection pressure on juveniles to put on weight quickly likely explains this ontogenetic variation (Beauchamp 2015). First, juveniles may allocate a greater proportion of time to foraging than adults, regardless of group size, because natural selection favors juveniles to gain mass quickly early in life. Indeed, access to food can influence important life history decisions, such as the timing of natal dispersal or the age of first reproduction. For example, in Belding’s ground squirrels (*Spermophilus beldingi*), increased energy acquisition by juveniles supports their rapid growth and experimental provisioning of male juveniles promotes early natal dispersal (Bachman 1993; Nunes and Holekamp 1996; Nunes et al. 1999). Second, our current findings are also consistent with the ecophysiology of anti-predator defenses in California ground squirrels. Specifically, whereas adults are largely resistant to rattlesnake venom, only older (heavier) juveniles mount sufficient defenses to survive rattlesnake bites (Poran and Coss 1990; Biardi et al. 1999, 2005). Thus, selection may be particularly strong on traits that allow juveniles to quickly gain mass sufficient for coping with rattlesnake venom should they be attacked.

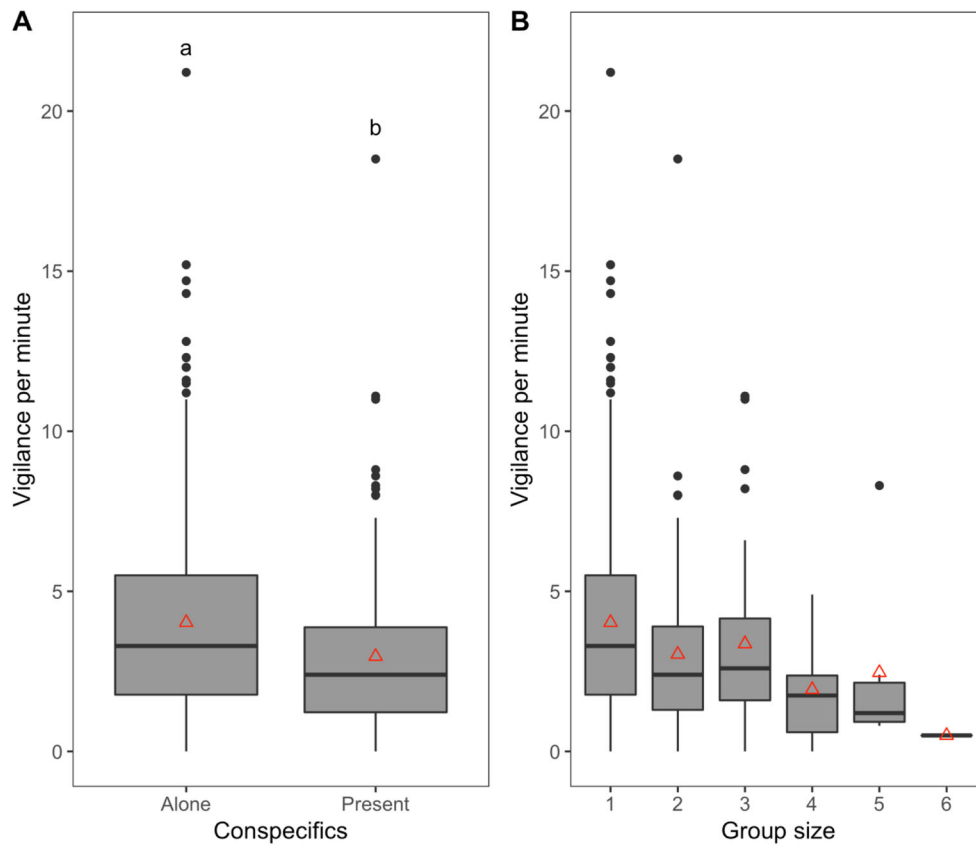


Fig. 4 The effect of **(A)** conspecific presence and **(B)** group size on rates of vigilance during foraging by focal California ground squirrels of all ages. Subjects either foraged alone (group sizes of one; $N = 240$ surveys) or foraged in groups comprised of two ($N = 90$ surveys), three ($N = 35$ surveys), four ($N = 14$ surveys), five ($N = 6$ surveys), and six ($N = 1$ survey) during focal animal sampling involving a total of 156 unique individuals. The middle quartile (dark line) represents the median; the

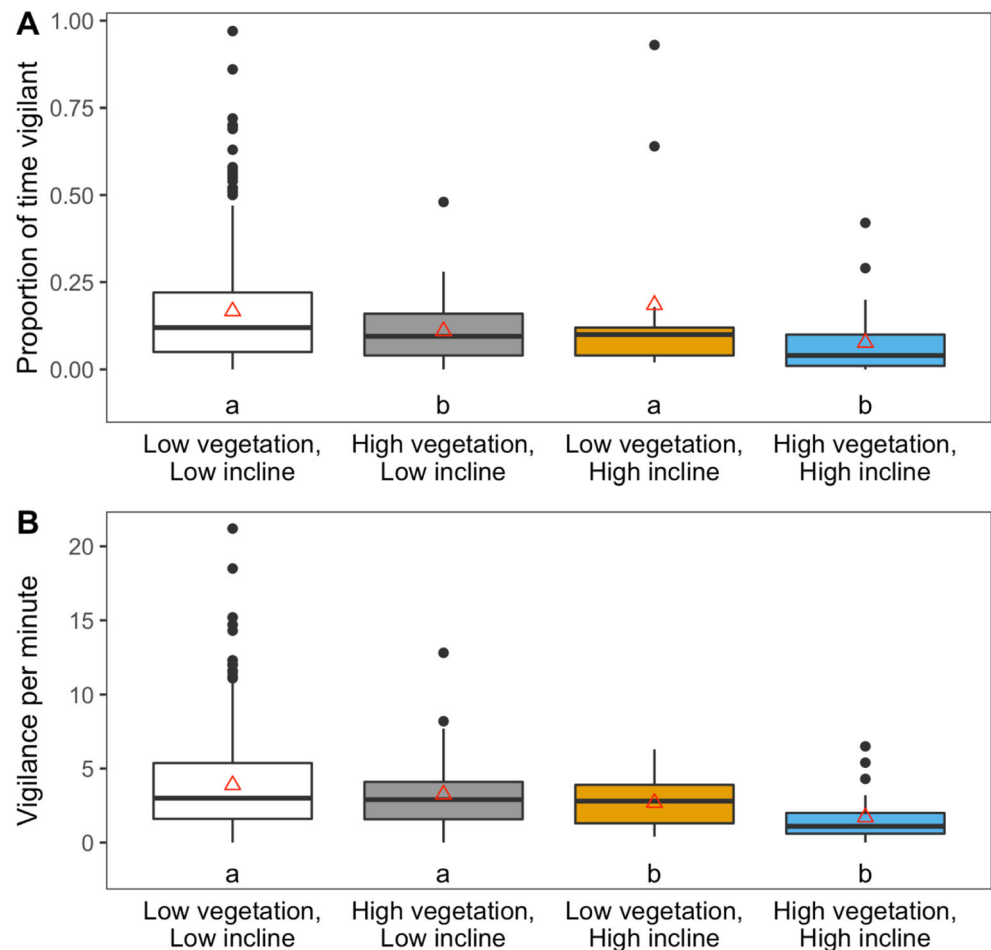
box edges are the upper and lower quartiles; the whiskers are 50% from the median, and the closed circles correspond to the outliers, calculated as the values smaller or larger than 1.5 times the box length (i.e., upper—lower quartile). Red triangles represent means. In panel **(A)**, different lowercase letters above boxes represent statistical differences between categories. In panel **(B)**, the group size effect was significant regardless of age category

Regardless of whether energetic demands, cognitive constraints, or a combination of both factors limit the responsiveness of juveniles to changing group sizes, our data suggest that juveniles likely compensate for this deficiency to some extent by, on average, occurring in significantly larger social groups than adults. This modest decrease in foraging group size—albeit it only from 1.7 to 1.4 individuals—from the juvenile to the adult stage is consistent with the notion that juveniles likely depend upon adult females for protection during foraging long after they are weaned. This is likely given that adult female California ground squirrels often intervene on behalf of juveniles by mobbing, throwing dirt at, and tail flagging at nearby rattlesnakes (Owings and Coss 1977), and the responsiveness of adult females to danger increases when they have dependent young (Leger and Owings 1978).

Additional data on the genetic relationships among individuals comprising foraging groups should offer insights into whether the selective forces of kin selection favor cooperative protection during foraging, as occurs in many other mammalian societies (Clutton-Brock 2002; Smith

2014). Juveniles in many other small- and medium-sized subterranean mammals benefit from increased vigilance by adult relatives (Arenz and Leger 2000; Hollén and Manser 2006). Juveniles also often maintain closer distances to safety than do adults and, thus, may mitigate danger by managing their space use (Boellstorff and Owings 1995). Future studies should investigate how proximity to kin within aboveground social networks and distance from refuges (burrows) shape foraging decisions in California ground squirrels. Moreover, the timing of our study may in part explain the lack of sex differences detected here. That is, our study focused on the months directly after the emergence of newly recruited juveniles, but sex differences in California ground squirrel responses to alarm calls disappear after young are weaned (Loughry and McDonough 1989). Thus, future studies could offer insights into the extent to which context-dependent vigilance varies with reproductive state, particularly for adult females with direct or indirect descendants that are still nursing. Such work could also inform our understanding of how the age-sex

Fig. 5 The effect of substrate angle and vegetation height on (A) proportion of time foraging and (B) rates of vigilance during foraging. The middle quartile (dark line) represents the median; the box edges are the upper and lower quartiles; the whiskers are 50% from the median, and the closed circles correspond to the outliers, calculated as the values smaller or larger than 1.5 times the box length (i.e., upper—lower quartile). Red triangles represent means. Different lowercase letters below boxes represent statistical differences between categories for each measure



composition (Childress and Lung 2003) and/or genetic relatedness of foraging groups (Olson et al. 2015) contribute to group-level differences in vigilance.

Ecological factors shape foraging decisions

Microhabitat features, and to some degree season, predicted patterns of vigilance regardless of an individual's age category, sex, or colony membership. Animals were generally least vigilant on high inclines (steep slopes), in high vegetation, and early in the season. Although colony failed to predict either measure of vigilance, animals were observed foraging most often in low vegetation and at low inclines in the more disturbed colony (Crow).

Our finding that California ground squirrels were least vigilant when foraging on inclines is consistent with the limited work on this topic. For example, yellow-bellied marmots (*Marmota flaviventris*; Blumstein et al. 2004) and Mongolian gerbils (*Meriones unguiculatus*; Embar et al. 2014) reduce their vigilance when foraging on the steepest slopes, presumably because they detect predators most efficiently. Some ungulates also forage on steep slopes but do so because they

benefit from reduced encounters with predators. This occurs in elk (*Cervus elaphus*) who forage on steep cliffs to avoid wolves (*C. lupus*) predation; wolves rarely hunt on mountains because hunting on slopes increases their risk of injury (Creel et al. 2005). Future research should inquire whether increased predator detection, reduced predation pressure, and/or a combination of both explain the observed reduction in vigilance by California ground squirrels on inclines.

Increased vigilance in low vegetation by California ground squirrels may reflect habitat-dependent variation in predation pressure and/or nutritional value of forage. As is common for rodents (Lima and Dill 1990; Longland and Price 1991; Tchabovsky et al. 2001; Smith and Batzli 2006; Verdolin 2006; Watson et al. 2007), California ground squirrels likely also suffer from increased predator-induced mortality when foraging in areas lacking sufficient vegetative cover. Future research is needed to assess factors contributing to individual differences in patterns of habitat selection in relation to habitat availability—and its associated fitness consequences for individuals—for this species. Despite the increased risk of foraging on preferred food items in open areas, dietary preferences may explain the

tendency for animals to forage in microhabitats with high predation risk. For example, the nutritional benefits gained from foraging in open areas may overwhelm the costs of increased risk of predation (Lima 1985). Foragers capable of caching seeds in cheek pouches may maximize energy efficiency by quickly gathering high-quality food in risky habitats and carrying food items to safety prior to consumption (Lima et al. 1985). This foraging method is likely particularly relevant for California ground squirrels given their extensive cheek pouches for their body size (Grinnell 1918). Field experiments that manipulate predator access (e.g., Byrom et al. 2000), nutritional value of forage (e.g., Desy et al. 1990), and vegetative cover (e.g., Smith and Batzli 2006) could offer insights into the mechanisms generating these patterns.

Taken together, our study demonstrates that multiple factors contribute to foraging decisions in the California ground squirrel. Conspecific presence, especially for adults, in combination with immediate ecological conditions (e.g., microhabitat, season), most strongly influence the foraging decisions for this facultatively social and ecologically flexible free-living mammal. Our findings highlight the importance of context in shaping the perception and management of risk by animals forced to integrate a suite of factors in variable environments.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All methods were approved by the Animal Care and Use Committee at Mills College and consistent with guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes and Gannon 2016). We conducted this work with permission from the California Department of Fish and Wildlife and East Bay Parks.

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References

- Arenz CL, Leger DW (2000) Antipredator vigilance of juvenile and adult thirteen-lined ground squirrels and the role of nutritional need. *Anim Behav* 59:535–541
- Ayon RE, Putman BJ, Clark RW (2017) Recent encounters with rattlesnakes enhance ground squirrel responsiveness to predator cues. *Behav Ecol Sociobiol* 71:149
- Bachman GC (1993) The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. *Anim Behav* 46:233–244
- Bakker VJ (2006) Microhabitat features influence the movements of red squirrels (*Tamiasciurus hudsonicus*) on unfamiliar ground. *J Mammal* 87(1):124–130
- Banks MS, Sprague WW, Schmoll J, Parnell JA, Love GD (2015) Why do animal eyes have pupils of different shapes? *Sci Adv* 1:e1500391
- Bates D, Mächler M, Bolker B, Walker S (2014) Fitting linear mixed-effects models using lme4. *arXiv* 1406:5823
- Beauchamp G (2008) What is the magnitude of the group-size effect on vigilance? *Behav Ecol* 19:1361–1368
- Beauchamp G (2015) *Animal vigilance: monitoring predators and competitors*. Academic Press, Oxford
- Beauchamp G (2018) The effect of age on vigilance: a longitudinal study with a precocial species. *Behaviour* 155:1011–1024
- Bednekoff PA, Blumstein DT (2009) Peripheral obstructions influence marmot vigilance: integrating observational and experimental results. *Behav Ecol* 20:1111–1117
- Bertram BCR (1978) Living in groups: predators and prey. In: Krebs JR, Davies NB (eds) *Behavioural ecology: an evolutionary approach*, 1st edn. Blackwell Scientific, Oxford, pp 64–96
- Biardi JE, Coss RG, Smith DG (1999) California ground squirrel (*Spermophilus beecheyi*) blood sera inhibits crotalid venom proteolytic activity. *Toxicon* 38:713–721
- Biardi JE, Chien DC, Coss RG (2005) California ground squirrel (*Spermophilus beecheyi*) defenses against rattlesnake venom digestive and hemostatic toxins. *J Chem Ecol* 31:2501–2518
- Blumstein DT, Daniel JC (2007) *Quantifying behavior the JWatcher way*. Sinauer Associates Incorporated, Massachusetts
- Blumstein DT, Runyan A, Seymour M, Nicodemus A, Ozgul A, Ransler F, Im S, Stark T, Zugmeyer C, Daniel JC (2004) Locomotor ability and wariness in yellow-bellied marmots. *Ethology* 110:615–634
- Boellstorff DE, Owings DH (1995) Home range, population structure, and spatial organization of California ground squirrels. *J Mammal* 76:551–561
- Boggs CL (1992) Resource allocation: exploring connections between foraging and life history. *Funct Ecol* 6:508–518
- Boland CR (2003) An experimental test of predator detection rates using groups of free-living emus. *Ethology* 109:209–222
- Byrom AE, Karels TJ, Krebs CJ, Boonstra R (2000) Experimental manipulation of predation and food supply of arctic ground squirrels in the boreal forest. *Can J Zool* 78:1309–1319
- Caro TM (2005) *Antipredator defenses in birds and mammals*. University of Chicago Press, Chicago
- Childress MJ, Lung MA (2003) Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Anim Behav* 66:389–398
- Chmura HE, Wey TW, Blumstein DT (2016) Assessing the sensitivity of foraging and vigilance to internal state and environmental variables in yellow-bellied marmots (*Marmota flaviventris*). *Behav Ecol Sociobiol* 70:1901–1910
- Clutton-Brock T (2002) Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296:69–72
- Cords M (1990) Vigilance and mixed-species association of some East African forest monkeys. *Behav Ecol Sociobiol* 26:297–300

- Coss RG (1991) Context and animal behavior III: the relationship between early development and evolutionary persistence of ground squirrel antismoke behavior. *Ecol Psychol* 3:277–315
- Cowlishaw G (1997) Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Anim Behav* 53:667–686
- Creel S, Winnie J, Maxwell B, Hamlin K, Creel M (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86:3387–3397
- Creel S, Christianson D, Liley S, Winnie JA (2007) Predation risk affects reproductive physiology and demography of elk. *Science* 315:960–960
- Dall SR, Giraldeau LA, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. *Trends Ecol Evol* 20:187–193
- Desy EA, Batzli GO, Liu J (1990) Effects of food and predation on behaviour of prairie voles: a field experiment. *Oikos* 58:159–168
- Dill LM (1987) Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. *Can J Zool* 65:803–811
- Dimond S, Lazarus J (1974) The problem of vigilance in animal life. *Brain Behav Evol* 9:60–79
- Elgar MA (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol Rev* 64:13–33
- Embar K, Kotler BP, Mukherjee S (2011) Risk management in optimal foragers: the effect of sightlines and predator type on patch use, time allocation, and vigilance in gerbils. *Oikos* 120:1657–1666
- Embar K, Raveh A, Burns D, Kotler BP (2014) To dare or not to dare? Risk management by owls in a predator–prey foraging game. *Oecologia* 175:825–834
- Fairbanks B, Dobson FS (2007) Mechanisms of the group-size effect on vigilance in Columbian ground squirrels: dilution versus detection. *Anim Behav* 73:115–123
- Favreau FR, Goldizen AW, Pays O (2010) Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. *Proc R Soc Lond B* 277:2089–2095
- Favreau FR, Pays O, Fritz H, Goulard M, Best EC, Goldizen AW (2015) Predators, food and social context shape the types of vigilance exhibited by kangaroos. *Anim Behav* 99:109–121
- FitzGibbon CD (1989) A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Anim Behav* 37:508–510
- Grinnell J (1918) Natural history of the ground squirrels of California. California State Printing Office, Sacramento
- Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol* 31:295–311
- Hanson MT, Coss RG (1997) Age differences in the response of California ground squirrels (*Spermophilus beecheyi*) to avian and mammalian predators. *J Comp Psychol* 111:174–184
- Hanson MT, Coss RG (2001) Age differences in arousal and vigilance in California ground squirrels (*Spermophilus beecheyi*). *Dev Psychobiol* 39:199–206
- Helfman GS (1989) Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behav Ecol Sociobiol* 24:47–58
- Hirsch BT (2002) Social monitoring and vigilance behavior in brown capuchin monkeys (*Cebus apella*). *Behav Ecol Sociobiol* 52:458–464
- Holekamp KE, Nunes S (1989) Seasonal variation in body weight, fat, and behavior of California ground squirrels (*Spermophilus beecheyi*). *Can J Zool* 67:1425–1433
- Hollén LI, Manser MB (2006) Ontogeny of alarm call responses in meerkats, *Suricata suricatta*: the roles of age, sex and nearby conspecifics. *Anim Behav* 72:1345–1353
- Kacelnik A, Bateson M (1996) Risky theories—the effects of variance on foraging decisions. *Am Zool* 36:402–434
- Koprowski JL (2002) Handling tree squirrels with a safe and efficient restraint. *Wildlife Soc B* 706:101–103
- Kutsukake N (2006) The context and quality of social relationships affect vigilance behaviour in wild chimpanzees. *Ethology* 112:581–591
- Lea AJ, Blumstein DT (2011) Age and sex influence marmot antipredator behavior during periods of heightened risk. *Behav Ecol Sociobiol* 65:1525–1533
- Leger DW, Owings DH (1978) Responses to alarm calls by California ground squirrels: effects of call structure and maternal status. *Behav Ecol Sociobiol* 3:177–186
- Leger DW, Owings DH, Coss RG (1983) Behavioral ecology of time allocation in California ground squirrels (*Spermophilus beecheyi*): microhabitat effects. *J Comp Psychol* 97:283–291
- Li Z, Jiang Z (2008) Group size effect on vigilance: evidence from Tibetan gazelle in Upper Buha River, Qinghai-Tibet Plateau. *Behav Process* 78:25–28
- Li C, Jiang Z, Li L, Li Z, Fang H, Li C, Beauchamp G (2012) Effects of reproductive status, social rank, sex and group size on vigilance patterns in Przewalski's gazelle. *PLoS One* 7:e32607
- Lima SL (1985) Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia* 66:60–67
- Lima SL, Bednekoff PA (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am Nat* 153:649–659
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Lima SL, Valone TJ, Caraco T (1985) Foraging-efficiency-predation-risk trade-off in the grey squirrel. *Anim Behav* 33:155–165
- Longland WS, Price MV (1991) Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? *Ecology* 72:2261–2273
- Loughry WJ, McDonough CM (1989) Calling and vigilance in California ground squirrels: age, sex and seasonal differences in responses to calls. *Am Midl Nat* 121:312–321
- Lung MA, Childress MJ (2006) The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. *Behav Ecol* 18:12–20
- McNamara JM, Houston AI (1992) Risk-sensitive foraging: a review of the theory. *Bull Math Biol* 54:355–378
- Metcalfe NB, Furness RW (1984) Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. *Behav Ecol Sociobiol* 15:203–206
- Milinski M, Heller R (1978) Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). *Nature* 275:642–644
- Nunes S, Holekamp KE (1996) Mass and fat influence the timing of natal dispersal in Belding's ground squirrels. *J Mammal* 77:807–817
- Nunes S, Duniec TR, Schweppe SA, Holekamp KE (1999) Energetic and endocrine mediation of natal dispersal behavior in Belding's ground squirrels. *Horm Behav* 35:113–124
- Olson RS, Haley PB, Dyer FC, Adami C (2015) Exploring the evolution of a trade-off between vigilance and foraging in group-living organisms. *R Soc Open Sci* 2:150135
- Owings DH, Coss RG (1977) Snake mobbing by California ground squirrels: adaptive variation and ontogeny. *Behaviour* 62:50–68
- Owings DH, Coss RG (1991) Context and animal behavior: I. Introduction and review of theoretical issues. *Ecol Psychol* 3:1–9
- Owings DH, Borchert M, Virginia R (1977) The behaviour of California ground squirrels. *Anim Behav* 25:221–230
- Pangle WM, Holekamp KE (2010) Functions of vigilance behaviour in a social carnivore, the spotted hyaena, *Crocuta crocuta*. *Anim Behav* 80:257–267
- Parker GA, Smith JM (1990) Optimality theory in evolutionary biology. *Nature* 348:27–33
- Pays O, Jarman PJ (2008) Does sex affect both individual and collective vigilance in social mammalian herbivores: the case of the eastern grey kangaroo? *Behav Ecol Sociobiol* 62:757–767

- Pays O, Renaud PC, Loisel P, Petit M, Gerard JF, Jarman PJ (2007) Prey synchronize their vigilant behaviour with other group members. *Phil Trans R Soc B* 274:1287–1291
- Poran NS, Coss DT (1990) Development of antisnake defenses in California ground squirrels (*Spermophilus beecheyi*): I. Behavioral and immunological relationships. *Behaviour* 112:222–245
- Poran NS, Coss RG, Benjamini ELI (1987) Resistance of California ground squirrels (*Spermophilus beecheyi*) to the venom of the northern Pacific rattlesnake (*Crotalus viridis oregonus*): a study of adaptive variation. *Toxicon* 25:767–777
- Powolny T, Bretagnolle V, Aguilar A, Eraud C (2014) Sex-related differences in the trade-off between foraging and vigilance in a granivorous forager. *PLoS One* 9:e101598
- Pulliam HR (1973) On the advantages of flocking. *J Theor Biol* 38:419–422
- Putman BJ, Coss RG, Clark RW (2015) The ontogeny of antipredator behavior: age differences in California ground squirrels (*Otospermophilus beecheyi*) at multiple stages of rattlesnake encounters. *Behav Ecol Sociobiol* 69:1447–1457
- R Development Core Team (2018) R: a language and environment for statistical computing. The R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Reboreda JC, Fernandez GJ (1997) Sexual, seasonal and group size differences in the allocation of time between vigilance and feeding in the greater rhea *Rhea americana*. *Ethology* 103:198–207
- Roberts G (1996) Why individual vigilance declines as group size increases. *Anim Behav* 51:1077–1086
- Ruckstuhl KE, Festa-Bianchet M, Jorgenson JT (2003) Bite rates in Rocky Mountain bighorn sheep (*Ovis canadensis*): effects of season, age, sex and reproductive status. *Behav Ecol Sociobiol* 54:167–173
- Schooley RL, Sharpe PB, Horne BV (1996) Can shrub cover increase predation risk for a desert rodent? *Can J Zool* 74:157–163
- Sharpe PB, Van Horne B (1998) Influence of habitat on behavior of Townsend's ground squirrels (*Spermophilus townsendii*). *J Mammal* 79:906–918
- Sih A (1980) Optimal behavior: can foragers balance two conflicting demands? *Science* 210:1041–1043
- Sikes RS, Gannon WL (2016) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J Mammal* 97:663–688
- Smith JE (2014) Hamilton's legacy: kinship, cooperation and social tolerance in mammalian groups. *Anim Behav* 92:291–304
- Smith JE, Batzli GE (2006) Dispersal and mortality of prairie voles (*Microtus ochrogaster*) in fragmented landscapes: a field experiment. *Oikos* 112:209–217
- Smith JE, Long DJ, Russel ID, Newcomb KL, Muñoz VD (2016) *Otospermophilus beecheyi* (Rodentia: Sciuridae). *Mamm Spec* 48: 1–18
- Smith JE, Gamboa DA, Spencer JM, Travenick SJ, Ortiz CA, Hunter RD, Sih A (2018) Split between two worlds: automated sensing reveals links between above- and belowground social networks in a free-living mammal. *Phil Trans R Soc B* 373:20170249
- Stamps JA (2007) Growth-mortality tradeoffs and 'personality traits' in animals. *Ecol Lett* 10:355–363
- Stephens DW (2008) Decision ecology: foraging and the ecology of animal decision making. *Cogn Affect Behav Ne* 8:475–484
- Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton
- Tchabovsky AV, Krasnov B, Khokhlova IS, Shenbrot GI (2001) The effect of vegetation cover on vigilance and foraging tactics in the fat sand rat *Psammomys obesus*. *J Ethol* 19:105–113
- Treves A (2000) Theory and method in studies of vigilance and aggregation. *Anim Behav* 60:711–722
- Verdolin JL (2006) Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behav Ecol Sociobiol* 60:457–464
- Watson M, Aebischer NJ, Cresswell W (2007) Vigilance and fitness in grey partridges *Perdix perdix*: the effects of group size and foraging-vigilance trade-offs on predation mortality. *J Anim Ecol* 76:211–221
- Werner EE, Anholt BR (1993) Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am Nat* 142:242–272
- Whiteside MA, Langley EJ, Madden JR (2016) Males and females differentially adjust vigilance levels as group size increases: effect on optimal group size. *Anim Behav* 118:11–18
- Xia C, Xu W, Yang W, Blank D, Qiao J, Liu W (2011) Seasonal and sexual variation in vigilance behavior of goitered gazelle (*Gazella subgutturosa*) in western China. *J Ethol* 29:443–451
- Yáber MC, Herrera EA (1994) Vigilance, group size and social status in capybaras. *Anim Behav* 48:1301–1307