

Group-enhanced predator detection and quality of vigilance in a social ground squirrel

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Animals may form groups for different reasons, and one major benefit of grouping in many species is reduced predation risk. In diurnal species, vigilance is used to detect predators, resulting in a trade-off between feeding activity and predation risk. Species can reduce the cost of this trade-off with low-quality vigilance – performing another behaviour while vigilant – in comparison to high-quality vigilance (only being vigilant). Two nonmutually exclusive hypotheses explaining an inverse relationship between individual vigilance and group size are the dilution effect, where predation risk decreases in larger groups, and collective detection, where larger groups have more individuals that may detect a predator. Two predictions that support collective detection but not the dilution effect are that (1) overall group (collective) vigilance will increase with increasing group size, even while individual vigilance decreases, and (2) at least one group member must be vigilant to detect potential danger and communicate that information to group members. To test these predictions, we recorded behavioural data on low- and high-quality vigilance and alarm calling in the gregarious Barbary ground squirrel, *Atlantoxerus getulus*. Barbary ground squirrels allocated more time to high-quality vigilance than low-quality vigilance. The collective detection hypothesis was partly supported: as group size increased, individual low- and high-quality vigilance did not decrease, but collective high-quality vigilance did increase. Furthermore, we found that repetitive alarm calling warned group members of terrestrial threats. Our results show that this invasive species displays specific antipredator behaviours to different aerial and terrestrial predators compared to predators in their endemic range. The low level of time allocated to low-quality vigilance indicates that natural selection strongly favours high-quality vigilance in this species despite the trade-off with foraging. Our study broadens our understanding of antipredator and risk-sensitive behaviour.

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A major benefit that can select for group living is predator avoidance through, for example, the use of group members as cover, enhanced information transfer among group members, cooperation among group members to deter predators, dilution of predation risk, or increased predator detection (Alexander, 1974; Bell, Radford, Rose, Wade, & Ridley, 2009; Bertram, 1978; Hamilton, 1971; Owings & Coss, 1977; Pulliam, 1973; Sherman, 1977; Waterman, 1997). Animals can use different cues – olfactory, auditory and visual – to detect predators (Blumstein, Barrow, & Luterra, 2008; Klump & Shalter, 1984; McNamara & Houston, 1992; Phillips & Waterman, 2013). Vigilance is a way to detect

visual cues associated with predators, especially in diurnal species (Ylönen & Brown, 2007).

The time spent vigilant is considered a cost of the trade-off between feeding activity and predation risk (Bednekoff & Lima, 1998), because foraging and vigilance are assumed to be exclusive (McNamara & Houston, 1992; Pulliam, 1973; but see ; Lima & Bednekoff, 1999). This trade-off may result in a difference in the quality of vigilance: individuals are either vigilant while performing another behaviour (nonexclusive, free or 'low-quality' vigilance) or are vigilant without performing any other behaviour (exclusive, costly or 'high-quality' vigilance) (Ebensperger, Hurtado, & Ramos-Jiliberto, 2006; Fairbanks & Dobson, 2007; Favreau et al., 2015; Fortin, Boyce, & Merrill, 2004; Kildaw, 1995; Pays, Jarman, Loisel, & Gerard, 2007; Unck, Waterman, Verburg, & Bateman, 2009). Conversely, the trade-off between feeding activity and predation risk may also affect the quality of foraging. Individuals may

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have some awareness of predators while performing other behaviours, i.e. 'apprehension' (Brown, Laundre, & Gurung, 1999), which can lead to a reduction in the quality of foraging. Yet, these animals are safer than when they are focused solely on foraging, because they are aware of their surroundings through low-quality vigilance (Kotler et al., 2002). In comparison, when individuals focus on vigilance (high-quality vigilance), they are much safer from predation than individuals performing low-quality vigilance, although they lose foraging opportunities (Dall, Kotler, & Bouskila, 2001).

Not only can the trade-off between foraging and vigilance influence predator detection, but so can group size. For example, social species may show an inverse relationship between individual vigilance and group size (Elgar, 1989). The hypotheses most often used to explain this relationship are the collective detection and dilution effect. The risk of predation decreases as the number of individuals increases in a group in the dilution effect hypothesis. This hypothesis predicts a negative relationship between individual vigilance and group size (Bertram, 1978; Roberts, 1996). Collective detection of predators is explained by a greater probability of detecting a predator with increasing group size – 'many-eyes' available for scanning (Lima, 1995; Lima & Dill, 1990; Pulliam, 1973). The predictions for the collective detection hypothesis are that, as group size increases, individual vigilance decreases, and yet overall group vigilance and detection ability increases (Lima, 1995; Lima & Dill, 1990; Pulliam, 1973). For the collective detection of predators to function, it is important that at least one individual is vigilant and detects a threat, upon which the alert individual transfers information of potential danger to its group members. Information transfer can occur, for example, when a vigilant individual alerts others by seeking cover, assuming that group members monitor conspecifics (Favreau, Goldizen, & Pays, 2010), or when an alert individual alarm signals to inform group members of potential danger (Fairbanks & Dobson, 2007). Alarm signals (e.g. alarm calls) not only inform group members of potential risk, but can also cause chaos, discourage an attack, attract other predators to aid in evading predation (Klump & Shalter, 1984), or reduce the patch quality for the predator as all group members are aware of the predator (Blumstein, 2007). Different predators can affect the behaviour of prey species diversely; therefore, alarm calls can also be informative about the predator type, e.g. aerial or terrestrial (Courter & Ritchison, 2010; Ducheminsky, Henzi, & Barrett, 2014; Macedonia, 1990; Macedonia & Evans, 1993). Other information about the threat can be transferred through, for example, differences in call bout duration or the number of callers (Blumstein, 2007; Blumstein, Verneyre, & Daniel, 2004; Sloan & Hare, 2004, 2008).

Even though it is difficult to disentangle the detection and dilution hypotheses, since both hypotheses are not mutually exclusive and could both explain grouping (Beauchamp, 2017), overall group vigilance is not predicted to increase with larger groups, nor do alarm calls play a role in the dilution effect hypothesis (Hamilton, 1971; Lima, 1995). Our research tests the predictions of the collective detection and dilution hypotheses for low- and high-quality vigilance in the Barbary ground squirrel, *Atlantoxerus getulus*, using the invasive island population on Fuerteventura, Spain. The small amount of information published on the social organization of Barbary ground squirrels indicates that they mainly live gregariously (Machado & Domínguez, 1982), although group composition varies throughout the year (Gouat & Yahyaoui, 2001). This species is diurnal (Machado & Domínguez, 1982); therefore, vigilance is one of their main means to detect predators (Ylönen & Brown, 2007). On the island, the only terrestrial predators are feral cats, *Felis catus* (Medina, López-Darias, Nogales, & García, 2008), while the aerial predators are the Eurasian buzzard, *Buteo buteo insularum*, the common raven, *Corvus corax*

canariensis, and the common kestrel, *Falco tinnunculus dacotiae* (López-Darias & Lobo, 2008). Barbary ground squirrels have been heard to vocalize (Machado, 1979), but whether these vocalizations are alarm calls to warn conspecifics of potential threat – predator presence – and whether their possible alarm calls differ in response to specific predators (aerial or terrestrial predators) has not been studied. Therefore, this study system is excellent to test predictions from the detection and dilution hypotheses. Our predictions are specified in Table 1.

METHODS

Study Site, Species and Trapping Protocol

We studied an invasive population of Barbary ground squirrels on the island of Fuerteventura, Canary Islands, Spain, from February to July 2014, January to July 2015 and January to June 2016. Fuerteventura is a volcanic island with an arid climate and semidesert habitats (Machado, 1979). Our three study sites were located on the surroundings of small ravines and cultivated areas (28°34'60"N, 13°58'0"W), hosting a xerophytic scrubland as the main vegetation. All three study sites were characterized by the abundance of rock walls (Machado, 1979), which function as shelter and lookouts for the Barbary ground squirrels (López-Darias & Lobo, 2008).

Adult squirrels were trapped once or twice a week during our field seasons using live traps (Tomahawk Co., WI, U.S.A.; 13 × 13 × 40 cm), which were baited with peanut butter. We covered the traps with cardboard, placed the traps as much as possible in the shade, checked them every 45 min, and did not trap when temperatures exceeded 25 °C to minimize (heat) stress for the squirrels. Since the squirrels were not in traps for longer than 45 min, we did not provide bedding, food or water. Trapping did not result in any injuries or death. We used a cone bag to handle the squirrels to minimize stress during handling (Koprowski, 2002). The squirrels were held in place by a Velcro strip behind the elbow joints of their front paws and their eyes were covered at all times during handling, which did not last longer than 10 min, to minimize stress. For individual identification, every squirrel received a sterile 0.1 g 2.1 × 12 mm passive integrated transponder (PIT) tag (Avid Inc., Norco, CA, U.S.A.), which was, on average, 0.05% of an adult squirrel's weight. These tags did not impede normal behaviour. All adults received a unique dorsal dye mark for identification at a distance (Melchior & Iwen, 1965). None of the squirrels showed adverse reactions to the dye. We recorded the sex of the squirrels upon capture. The density of squirrels per hectare was 14.15, 9.19 and 7.24 for site 1, 2 and 3, respectively (details on the number of trapped and marked squirrels are provided in Appendix Table A1). All procedures were approved by the University of Manitoba Animal Care and Use Committee (protocol no. F14-032), were permitted by the government of Fuerteventura (Cabildo Insular de Fuerteventura no. 14885) and conformed to ASAB/ABS's guidelines for ethical research with animals.

Vigilance and Group Size

To quantify low- and high-quality vigilance, we performed scan sampling (Altmann, 1974), consisting of 10 min scans, throughout our field seasons. We conducted behavioural observations between 1000 hours GMT, when squirrels emerged from their sleeping burrows, and 2 h before sunset, when squirrels retreated into their burrows for the night (Machado, 1979). Squirrels were observed from roads and nearby elevated areas at distances (approximately 50 m) that did not affect ground squirrel behaviour. Behavioural data were collected using 'Numbers' (Apple, Cupertino, CA, U.S.A.) and 'Prim8' software (McDonald & Johnson, 2014) on an iPod and

Table 1

Hypotheses and predictions on vigilance behaviour and alarm communication in the Barbary ground squirrel

Hypothesis	Prediction	Source
Benefits of grouping		
Dilution	Individual vigilance decreases with larger groups	Bertram (1978)
Collective detection	Individual vigilance decreases with larger groups	Pulliam (1973)
	Overall vigilance increases with larger groups	Pulliam (1973)
	Alarm communication to warn group members of danger	Hamilton (1971)
Alarm communication		
Information on predator threats	Duration of alarm calls will be longer in presence of a predator	Blumstein (2007); Warkentin, Keeley, & Hare (2001)
is conveyed in alarm calls	Proportion of callers will be higher in presence of a predator	Blumstein et al. (2004); Sloan & Hare (2008)

Sources refer to the origin of the predictions.

an Android phone (Motorola Droid A850), respectively. We defined high-quality vigilance as scanning the environment from raised positions (>30 cm above ground) for more than 30 s (Manser, 1999). We measured the height of the rock walls and dams that were used by the squirrels as promontories when performing high-quality vigilance with a tape measure. Low-quality vigilance was considered as vigilance that lasted less than 30 s or was performed while doing other behaviours (Makenbach, Waterman, & Roth, 2013); therefore, we did not measure the duration of the low-quality vigilance bouts during scan sampling. Instead, we performed 10 min focal follow sampling (Altmann, 1974) to record duration of low-quality vigilance. We recorded the duration of low- and high-quality vigilance for 81 individuals (range 1–7 focal follows per individual) in 2015, which we analysed using a Wilcoxon signed-rank test. We also used the focal follows to test for an effect of wind on individual vigilance levels. We measured wind speed (km/h) after each focal follow with a Kestrel Weather Meter (Nielsen-Kellerman, Boothwyn, PA, U.S.A.). We performed a generalized linear mixed model (GLMM) using the package 'glmmADMB' with the beta distribution and identity (ID) as random factor, because we had multiple focal follows per ID (Bolker, Skaug, Magnusson, & Nielsen, 2012; Fournier et al., 2012).

In our vigilance and group size analysis, we excluded unknown individuals, days when females were in oestrus, observation periods when a predator was present and observation periods of less than 1 h, resulting in data for 64 individuals that were observed over 184 observation periods. Individual vigilance was calculated as the number of scans when an individual was performing low- or high-quality vigilance divided by the total scans in which the individual was observed. We only used individuals that were observed at least five times (5 different observation periods) in at least five scans per observation period (after Edwards & Waterman, 2011). We tested for a sex difference in time allocation for individual low- or high-quality vigilance using Mann–Whitney *U* tests, because of the non-normality of our vigilance data. We measured collective vigilance as the number of scans when at least one squirrel was performing low- or high-quality vigilance in the group divided by the time each group was observed.

We defined a group as individuals that were in each other's visible range during an observation period (Stankowich, 2003). We measured the ground squirrel's visible range using an object of the same height as a ground squirrel vertically stretched on its hind-legs, whereby the object was moved over the ground until it was no longer visible (Edwards & Waterman, 2011), which occurred at a distance of 60 m. We included squirrels on the ground and on rock walls. To find out whether a 60 m radius for group membership is biologically relevant, we tested for an effect of the proportion of time spent vigilant for group sizes within 10 m or 60 m of a focal follow. Since we had multiple focal follows per individual we were able to perform a Wilcoxon signed-rank test on the number of conspecifics within 10 m or within 60 m on levels of low- and high-quality vigilance.

Often the relationship between vigilance and group size is analysed using least squares regression, although the relationship may not be linear or heteroscedasticity may be present (Blumstein, Daniel, & Evans, 2001; Dehn, 1990). When there is heteroscedasticity in the data, indicating that factors other than group size may influence the level of vigilance, then the use of quantile regression over linear regression to test for the relationship between vigilance and group size is suggested (Beauchamp, 2013). Quantiles or percentiles are commonly used in descriptive statistics, but not as a statistical tool in behavioural ecology (for examples see Chamaillé-Jammes & Blumstein, 2012; Korstjens, Lehmann, & Dunbar, 2010). Quantile regression estimates multiple slopes instead of only the slope of the conditional mean as in linear regression (Cade & Noon, 2003; Cade, Terrell, & Schroeder, 1999). The quantile regression estimate will indicate whether the level of vigilance for a specified quantile changes for every increase of group size by one individual, which indicates whether some levels of vigilance are more affected by group size than others. The relationship between vigilance and group size can be explained by the slopes of the lower quantiles if there is a positive interaction with an unknown factor, while the relationship can be explained by the slopes of the higher quantiles if there is a negative interaction with an unknown factor (Beauchamp, 2013; Cade, Noon, & Flather, 2005). As individual and collective low- and high-quality vigilance in our study did not show a constant variance, we used quantile regression as an appropriate alternative test to a least squares regression.

We used linear quantile mixed models (function 'lqmm') using the package 'lqmm' in R (Geraci, 2014) to test for a relationship between individual or collective low- or high-quality vigilance and group size. We included ID as a random factor in our individual low- and high-quality vigilance models, because we had multiple measurements per ID in our individual vigilance calculations. We included site as a random factor in our collective low- and high-quality vigilance models, because we had multiple measurements for each site in our collective vigilance measurements. We set the arguments and corresponding values to default. Following Beauchamp (2013), we set our quantiles (tau) to 0.2, 0.5 (i.e. median) and 0.8. We compared the random intercept and slope models using Akaike's information criterion (AIC), and selected the model with the lowest AIC in our analyses. The random intercept and slope models test whether intercepts or slopes differ from 0. We increased the optimized tolerance to 1e-3 and the maximum iterations to 1000 to avoid a convergence warning of the lower loop for all models, except the collective high-quality vigilance model. The total variation explained by the random factors ID and site for individual and collective vigilance, respectively, is called the intraclass correlation coefficient (ICC).

Response to Predator Encounters

We recorded antipredator behaviour after predator encounters using all-occurrence sampling (Altmann, 1974) throughout our field

season. We noted any predators (see Introduction) present or flying over and whether they attacked or were successful in their attack during our behavioural observations. Additionally, we recorded domestic dogs, *Canis lupus familiaris*, and unknown humans, as they can elicit alarm responses (Furrer & Manser, 2009). Barbary ground squirrels did not perceive the human observers that regularly visited the sites as a threat, i.e. the squirrels did not change their behaviour when the observer(s) arrived. We also recorded if heterospecific species (common hoopoe, *Upupa epops*; great grey shrike, *Lanius excubitor*; houbara bustard, *Chlamydotis undulata*; Spanish sparrow, *Passer hispaniolensis*) alarm-called prior to Barbary ground squirrel alarm calls. Since we had observation bias (Appendix Table A2), we divided the number of predators by total hours observed per site. We tested whether the predator (aerial, terrestrial, or both combined) observations differed per site using Pearson's chi-square tests. We considered terrestrial predators a 'high urgency' threat when they were observed within 30 m of the alarm caller or a 'low urgency' threat when they appeared at more than 30 m of the caller (Furrer & Manser, 2009). Aerial predators were assumed to be a threat when they flew to or away from a perch location or were perched in the site, all within 100 m of the alarm caller (Furrer & Manser, 2009).

We heard two different types of alarm calls: (1) a single whistle, which was produced by a mother with just-emerged offspring when an aerial predator attacked (heard on only three occasions, and not further discussed here); and (2) an alarm call that was a repeated vocalization, which we called a 'repeated bark'. We recorded 239 repeated alarm calls over a 3-year period. These alarm calls were considered repetitive, because five or more syllables were repeated at a similar rate (Owings, Hennessy, Leger, & Gladney, 1986). We recorded the identification of the caller and the duration of the alarm call once a ground squirrel started to call. We used a Z test to analyse whether aerial or terrestrial predators elicited the repeated barks. Call duration and proportion of callers (i.e. number of callers/total group size) violated the assumptions for parametric tests; therefore, we performed a Spearman rank correlation on call duration and group size. We used Kruskal–Wallis χ^2 to analyse differences in call duration and proportion of callers for different call-eliciting sources (terrestrial and aerial predators, heterospecific species, and not observed). If the Kruskal–Wallis test was significant, we used a post hoc test using the Hochberg correction (Hochberg, 1988). We used Wilcoxon two-sample tests to detect differences in call duration and proportion of callers when predators were 'high urgency' or 'low urgency' threats.

All statistical analyses were performed in R v.3.4.1 (R Core Team, 2017) and the significance level was set at $P \leq 0.05$. All figures were designed in the R package 'ggplot2' (Wickham, 2009).

RESULTS

Vigilance and Group Size

For the daily activity budget on vigilance, we used 410 observation hours. On average, our observation periods ($N = 399$) lasted 100 ± 73 min ($\bar{X} \pm \text{SD}$) (see Appendix Table A2 for a breakdown per site). Adult squirrels spent $39.8 \pm 1.6\%$ ($\bar{X} \pm \text{SE}$) of their time in high-quality vigilance, while $2.1 \pm 0.7\%$ ($\bar{X} \pm \text{SE}$) of their time was spent in low-quality vigilance. We found no sex differences for proportion time spent in high- and low-quality vigilance ($N = 67$ adult males and 91 adult females; high-quality: $38.4 \pm 2.5\%$ for males and $40.8 \pm 2.1\%$ for females ($\bar{X} \pm \text{SE}$); Mann–Whitney U test: $U = 4090.5$, $P = 0.07$; low-quality: $2.8 \pm 1.7\%$ for males and $1.5 \pm 0.3\%$ for females ($\bar{X} \pm \text{SE}$); Mann–Whitney U test: $U = 3301.5$, $P = 0.08$). Using our scan samples, the mean ($\pm \text{SE}$) high-quality vigilance bout duration was 264.0 ± 21.1 s (range 31–16516 s).

Averaged height of the promontories used by high-quality vigilant squirrels was 1.23 ± 0.03 m, ranging from 0.30 to 3.00 m ($N = 224$).

Our measurement of high-quality vigilance bouts in our focal data were constrained, as many high-quality vigilance bouts were longer than our 10 min focal follows. To compare between low- and high-quality vigilance bouts, we only included high-quality vigilance bouts that were less than 10 min. Even so, in our focal follows, the average duration of low-quality vigilance bouts (16.8 ± 0.7 s, $N = 412$ vigilance bouts from 73 individuals) were shorter than our high-quality vigilance bouts (88.5 ± 4.5 s, $N = 249$ bouts from 73 individuals; Wilcoxon signed-rank test: $V = 2278$, $P < 0.001$, $N = 67$ individuals who displayed both low- and high-quality vigilance). Wind speed did not affect individual low-quality vigilance (GLMM: $\chi^2_1 = 1.47$, $N = 74$ individuals, $P = 0.23$), nor high-quality vigilance (GLMM: $\chi^2_1 = 0.78$, $N = 77$ individuals, $P = 0.38$) in our focal follows. Therefore, we did not add wind to our models on group-size effect. We also did not find a difference in proportion of time spent in individual low-quality vigilance when conspecifics were within 10 m or 60 m ($8.8 \pm 6.6\%$ and $8.2 \pm 1.1\%$, $N = 28$; Wilcoxon signed-rank test: $V = 182.5$, $P = 0.65$), nor for individual high-quality vigilance (<10 m: $33.1 \pm 4.2\%$; <60 m: $42.5 \pm 4.3\%$, $N = 28$; $V = 275$, $P = 0.10$) in our focal follows. Therefore, we measured group size as conspecifics present within 60 m in our individual low- and high-quality vigilance models.

For our vigilance and group size analysis, we used 390 h of observations. On average, we observed 4.2 ± 0.1 ($\bar{X} \pm \text{SE}$) individuals per 10 min scan (range 1–14 squirrels/scan). Since high-quality vigilance bouts can last longer than one 10 min scan, we used total individuals observed during an observation period as group size. Per observation period, we observed 8.9 ± 0.4 ($\bar{X} \pm \text{SE}$) individuals ($N = 299$ observation periods). The AICs were lower for the quantiles of the random intercept model for individual high-quality vigilance, and for the quantiles of the random slope model for the individual low-quality and collective low- and high-quality models (Table 2). Individual time spent in low-quality vigilance did not decrease for any of the quantiles with increasing group size (Table 2, Fig. 1a). Individual high-quality vigilance decreased significantly by 2.4% with an increase in group size by one squirrel for the lower quantile ($\tau = 0.2$), did not decrease for the median ($\tau = 0.5$) and increased significantly by 1.2% for the upper quantile ($\tau = 0.8$; Table 2, Fig. 1b). Collective time spent in low-quality vigilance only increased significantly by 1.0% for the upper quantile, but did not increase for the lower and median quantiles (Table 2, Fig. 1c). Collective high-quality vigilance increased significantly for the 0.5 and 0.8 quantiles by 2.3 and 3.8%, respectively, for every increase in group size by one squirrel, but did not increase for the lower quantile (Table 2, Fig. 1d).

Response to Predator Encounters

We recorded 271 predator sightings during our behavioural observations ($N = 175$ aerial and $N = 96$ terrestrial predators). The rate of predator encounters did not differ per site (chi-square test: aerial predators: $\chi^2_2 = 0.03$, $P = 0.99$; terrestrial predators: $\chi^2_2 = 0.13$, $P = 0.94$; all predators: $\chi^2_2 = 0.03$, $P = 0.99$; Table 3). The eliciting sources of the repeated barks were either a bird of prey perched on or close to the ground ($N = 3$), a heterospecific (other species that do not prey upon the squirrels, $N = 5$), a terrestrial species (unknown human, $N = 3$; dog, $N = 3$; or feral cat, $N = 68$), or an unknown source (call-eliciting source not observed, $N = 162$). Taking all predator sightings into account, terrestrial predators almost always elicited the repeated barks (83.5% of the terrestrial predator sightings), while aerial predators only occasionally elicited repeated barks (6.4% of the aerial predator sightings; Z test: $Z = -3.15$, $P < 0.001$). We observed a 50% success rate for aerial

Table 2

Quantile regression mixed model (LQMM) results for the quantiles (τ) of 0.2, 0.5 and 0.8 of individual time spent in low- and high-quality vigilance, and collective time spent in low- and high-quality vigilance for Barbary ground squirrels

	$\tau = 0.2$			$\tau = 0.5$ (median)			$\tau = 0.8$		
	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
Individual low-quality vigilance									
Intercept	−0.001	0.005	0.87	−0.001	0.006	0.87	−0.001	0.006	0.88
Slope	0.000	0.001	0.90	0.000	0.001	0.87	0.000	0.001	0.86
ICC	0.985			0.980			0.944		
AIC intercept model	−5826.71			−5087.93			−3639.30		
AIC slope model	−5724.52			−4985.74			−3537.10		
Individual high-quality vigilance									
Intercept	0.381	0.049	<0.001	0.424	0.045	<0.001	0.463	0.049	<0.001
Slope	−0.024	0.004	<0.001	−0.008	0.005	0.16	0.012	0.005	0.03
ICC	0.573			0.627			0.515		
AIC intercept model	201.48			125.69			356.65		
AIC slope model	303.68			227.89			458.85		
Collective low-quality vigilance									
Intercept	0.005	0.033	0.88	0.005	0.008	0.55	0.006	0.009	0.50
Slope	−0.001	0.224	1.00	−0.001	0.001	0.65	0.010	0.003	0.001
ICC	0.931			0.912			0.798		
AIC intercept model	−767.86			−615.70			−330.32		
AIC slope model	−761.16			−609.00			−323.63		
Collective high-quality vigilance									
Intercept	0.585	0.108	<0.001	0.598	0.071	<0.001	0.615	0.075	<0.001
Slope	0.006	0.399	0.99	0.023	0.007	0.002	0.038	0.012	0.003
ICC	0.610			0.704			0.647		
AIC intercept model	−16.52			−99.19			−68.35		
AIC slope model	−9.82			−92.49			−61.66		

The intercept, slope and intraclass correlation coefficient (ICC) values are presented for the model with the lowest AIC values. Values in bold have a $P < 0.05$.

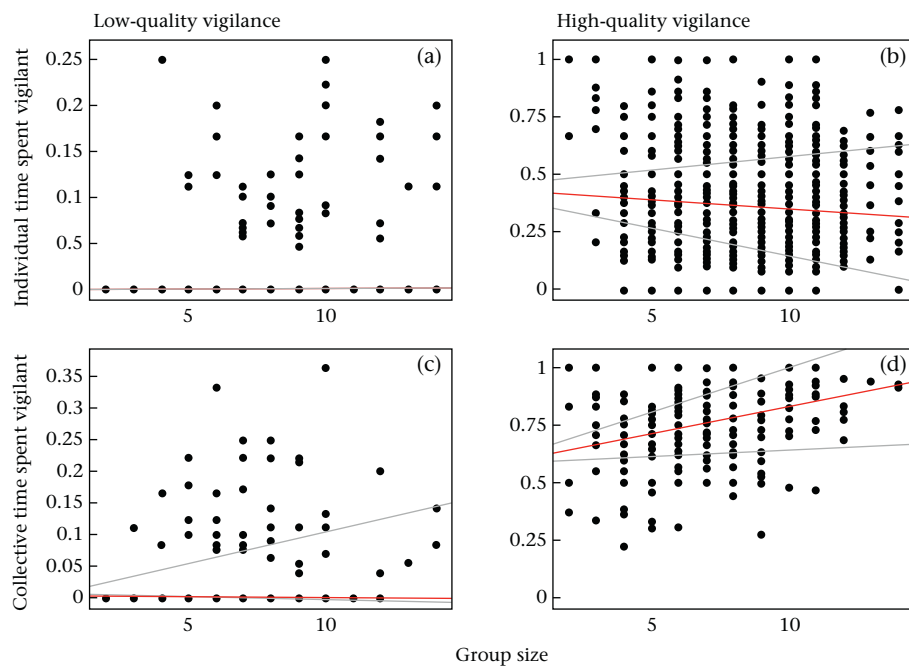


Figure 1. Quantile regression of individual (a) low-quality and (b) high-quality vigilance on group size, and of collective (c) low-quality and (d) high-quality vigilance on group size in Barbary ground squirrels. The solid grey regression lines represent the 0.2 and 0.8 quantiles, and the solid red regression line represents the 0.5 (median) quantile. Note the different Y scales for low- and high-quality vigilance.

predators ($N = 10$ observed aerial predator attacks) and a 25% success rate for terrestrial predators ($N = 4$ observed terrestrial predation events). We did have individuals disappear from the study over time, but the causes leading to their disappearance were unknown.

In 78% of the occurrences, calling individuals were located on top of rock walls or other promontories (elevated position at least 30 cm above ground) when a terrestrial predator was present in the

site. Call duration was 339.1 ± 20.7 s ($\bar{X} \pm \text{SE}$, $N = 239$), ranging from 1 s to 2024 s (up to 30 min), and on average $20.0 \pm 1.0\%$ ($\bar{X} \pm \text{SE}$) of the group members called (range 6–100% of the group members). Call duration was longer with increasing group size (Spearman rank correlation: $r_s = 0.22$, $N = 239$, $P < 0.001$; group size range 1–18). Call duration differed per eliciting call source (Kruskal–Wallis test: $H_3 = 17.49$, $P < 0.001$; Fig. 2a), whereas the proportion of callers did not (Kruskal–Wallis test: $H_3 = 6.59$,

Table 3

Predator sightings per hour (adjusted by observation hours per site) on Fuerteventura, Canary Islands, Spain for the years 2014–2016

Predation rate	Site 1	Site 2	Site 3
Aerial	0.20	0.23	0.32
Terrestrial	0.21	0.05	0.08
Total	0.41	0.28	0.40

$P = 0.09$; Fig. 2b). Call duration was longer for terrestrial predators compared to the ‘not observed’ call-eliciting source (post hoc test: $P < 0.001$; Fig. 2a), but we found no significant differences in call duration between heterospecific nonpredators ($N = 4$) and aerial predators ($N = 3$), possibly due to low sample sizes. Whether the predators were near (<30 m or ‘high risk’) or far (≥ 30 m or ‘low risk’) did not affect call duration (Wilcoxon two-sample test: $W = 243.5$, $N = 45$, $P = 0.69$) or proportion of callers ($W = 279$, $N = 10$, $P = 0.24$).

DISCUSSION

Our research found that collective high-quality vigilance increased with larger groups in the Barbary ground squirrel, supporting the collective detection hypothesis (Pulliam, 1973). This positive relationship between collective vigilance and group size is also found in some bird and other mammalian species (Bertram, 1980; Ebensperger et al., 2006; Lazarus & Lazarus, 1979; Li, Beauchamp, Wang, & Cui, 2016; Pays et al., 2007a,b; Pays, Sirot, & Fritz, 2012). Collective detection of predators also assumes that at least one individual is able to warn its group members of danger. We found that Barbary ground squirrels use repeated alarm calls to warn group members. Longer call duration informed group members of a terrestrial predator.

Contrary to our predictions that individual vigilance decreases and collective vigilance increases with increasing group size, Barbary ground squirrels did not decrease their individual low- and high-quality vigilance, nor did they increase their collective low-quality vigilance, in larger groups. Instead, our results indicate that variation in vigilance levels increased with larger groups. The random factors ID and site for individual and collective high-quality vigilance portray this increase in variation, because they explained between 50 and 70% of the variation, respectively (Table 2). In some bird and mammal species, the lack of relationship between collective low-quality vigilance and individual low- and high- quality vigilance and group size is also empirically supported (Catterall, Elgar, & Kikkawa, 1992; Favreau et al., 2010;

Fernández, Capurro, & Rebores, 2003; Quenette & Gerard, 1992; Treves, Drescher, & Ingrisano, 2001).

Different caveats of our study could explain the lack of a group size effect. First, our definition of group size may not have been the most appropriate. Group size was measured over a large area relative to the small Barbary ground squirrels. Often studies on smaller mammals use a threshold of 10 m for inclusion of individuals to a group (Blumstein et al., 2001), while larger mammals, such as red kangaroos, *Macropus rufus*, use a larger radius (Blumstein & Daniel, 2003). Therefore, our threshold of 60 m could have impacted our results. However, individuals performing high-quality vigilance were located on average more than 1 m above ground, suggesting that their field of view is more similar to larger mammals. Hence, the impact of our group size definition might not be too severe for our results on high-quality vigilance. However, for individuals performing low-quality vigilance, our threshold may prove too large, because the numerous rock walls and dams that provide lookouts (López-Darías & Lobo, 2008; Machado, 1979) prevent squirrels on the ground from seeing in the distance. Consequently, this scenario may also explain the result that Barbary ground squirrels only allocated 2% of their activity budget to low-quality vigilance. Hence, the squirrels may need to perform high-quality vigilance from raised positions to see in the distance, resulting in natural selection strongly favouring high-quality vigilance despite the trade-off it imposes with foraging. The time allocated to low- and high-quality vigilance is in contrast to the closely related Cape ground squirrels, *Xerus inauris*, where individuals perform mainly low-quality vigilance, but increase their high-quality vigilance in higher-risk habitat (Unck et al., 2009). This disparity in time allocation is possibly due to habitat differences. Cape ground squirrels live in very open habitats (Waterman, 1995), while the habitat of Barbary ground squirrels is interspersed with rock walls.

Second, the lack of relationship for individual and collective low-quality vigilance and group size may also be explained by our behavioural sampling method (Hirschler, Gedert, Majors, Townsend, & Hoogland, 2016). During a 10 min scan, the observer may have missed a low-quality vigilance event, but not a high-quality vigilance state. Individuals performing high-quality vigilance were more conspicuous, e.g. high-quality vigilant squirrels were situated on top of a rock wall for extended periods (>30 s). Thus, the scan sampling method could have resulted in the low proportion of individual and collective low-quality vigilance and, consequently, reduced statistical power (Beauchamp, 2013). Therefore, additional sampling may have been necessary to detect group-size effects on low-quality vigilance.

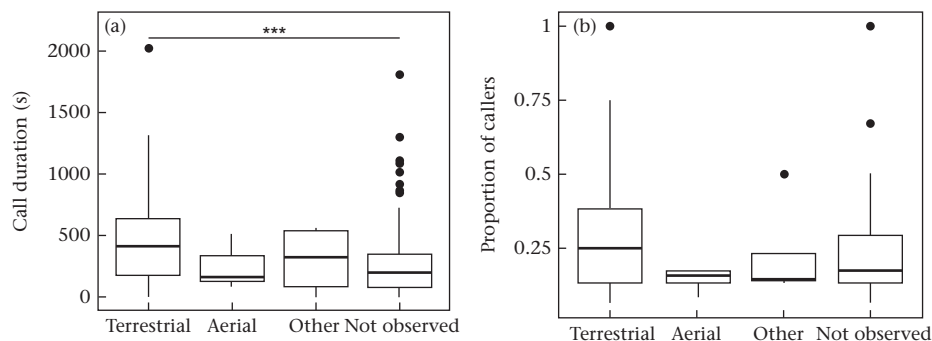


Figure 2. (a) Call duration and (b) proportion of callers for Barbary ground squirrels when aerial and terrestrial predators were present. The call-eliciting source ‘other’ included heterospecific species. ‘Not observed’ refers to situations when predators or heterospecific species were not observed. 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). Significant differences are denoted by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Besides our caveats, there are multiple explanations for the absence of the group size effect and for the result that individuals or groups at the extremes of the vigilance levels (0.2 and 0.8 quantiles) are more affected by group size. For example, sex has been found to influence vigilance in some group-living species (Li et al., 2012; Pays et al., 2012; Rieucau et al., 2012; Whiteside, Langley, & Madden, 2016). However, we found no sex differences in low- or high-quality vigilance, suggesting that sex does not interact with vigilance and group size in Barbary ground squirrels. Wind may also affect vigilance levels, because wind can be considered an ambient noise that affects the signal-to-noise ratio of sound (Bradbury & Vehrencamp, 1998; Hayes & Huntly, 2005) and, therefore, may affect the ability of prey animals to hear predators. The island is known for its strong trade winds (Marzol Jaén, 1988), with an average wind speed during our field work of 16.4 km/h. However, wind did not affect individual vigilance levels in our focal follows, suggesting that wind does not have a large effect on vigilance in Barbary ground squirrels.

Another explanation for the absence of a group size effect on the level of vigilance is that individuals may not only monitor for predators, but also monitor their group members, i.e. social vigilance (Bekoff, 1995; Lima, 1995; Fernández-Juricic, Smith, & Kacelnik, 2005; Favreau et al., 2010; Beauchamp, 2013). Unfortunately, we cannot disentangle predator from social vigilance in our study because we did not take gaze or head direction into consideration. However, gaze direction would have been difficult to distinguish due to the eye position of Barbary ground squirrels, as is seen in Gunnison's prairie dogs, *Cynomys gunnisoni* (Hirschler et al., 2016).

In addition to monitoring group members and scanning for predators, private information may be more valuable than public information, which can explain the absence of a group-size effect. Public information is often used in social foraging species, where individuals use information from group members to assess their environment, e.g. food patch quality (Valone, 1989). If one's own experience with food patch quality, i.e. private information (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005), is more beneficial than observing group members, then the group-size effect may be absent. Vigilance in eastern grey kangaroos, *Macropus giganteus*, is used both in social and antipredator contexts. When patch quality is rich, social low-quality vigilance increases, but when food patch quality is poor, antipredator low-quality vigilance decreases (Favreau et al., 2015). The dilution and detection hypotheses were supported in that study, because individual high-quality vigilance decreased with increasing group size. However, individual low-quality vigilance increased with increasing group size when food patch quality was poor (Favreau et al., 2015). This latter study shows that the relationship between vigilance and group size is not straightforward. Information gained either privately or publicly on patch quality may also prove important in Barbary ground squirrels. Even though we performed our study in winter and spring when food resources are at their highest on the island, these resources can be clumped, especially when fig and mulberry trees bear fruit. Thus, the spatial distribution of resources could affect foraging and consequently vigilance.

Besides the spatial distribution of resources, the spatial distribution of group members can be another reason for the absence of the group-size effect, because predators may have a preference for attacking peripheral individuals or may attack larger groups disproportionately. Semipalmated sandpipers, *Calidris pusilla*, increase their vigilance at the most risky edge of the group compared to the centre or the nonrisky edge of the group, because predators always arrive from a similar direction (Beauchamp & Ruxton, 2008). Adult female elk, *Cervus elaphus*, increase their vigilance not only with decreasing group size, but also when they are

positioned at the edge of the group where there is increased predation risk (Lung & Childress, 2007). Unfortunately, we did not take the position of the squirrels into consideration, so we cannot answer whether vigilance levels differ per position within the group. In our study, the rate of predation adjusted by the hours observed in each site did not differ, suggesting that habitat risk in terms of predation pressure does not explain the absence of a group-size effect.

A final explanation of the absence of a group-size effect is that individuals may imitate one another in the group (Michelena & Deneubourg, 2011; Pays et al., 2007a,b), and synchronize their vigilance bouts (Favreau et al., 2010; Fernández et al., 2003; Li et al., 2016; Pays, Dubot, Jarman, Loisel, & Goldizen, 2009; Pays et al., 2012; Podgórski et al., 2016). Synchronization may occur because vigilance levels of group members convey the group's fear level ('contagion-of-fear' hypothesis) (Beauchamp, 2015b). Synchronization can also occur when predators target individuals that are last to find cover. In this situation, individuals benefit by detecting predators before others do, so they can reach safety first ('predator targeting behaviour' hypothesis) (Beauchamp, 2015b; Sirot & Touzalin, 2009). Synchronization of vigilance bouts may also explain our result that, at the 0.8 quantile, individual high-quality vigilance increases with increasing group size.

Even though a group-size effect was absent for individual low- and high-quality and collective low-quality vigilance, collective high-quality vigilance increased with larger groups, and alarm communication was important in Barbary ground squirrels, supporting the presence of collective detection as an antipredator strategy. We found that mainly terrestrial predators elicited repeated barks in Barbary ground squirrels. A single alarm vocalization (whistle) was heard when an aerial predator attacked. Thus, our findings suggest that alarm calls reflect the urgency to respond (Macedonia & Evans, 1993; Manser, 2001), consistent with the literature for species living in open habitats (Furrer & Manser, 2009; Harris, Murie, & Duncan, 1983; Waring, 1966). Barbary ground squirrels produce tonic calls (repeated barks), which can last up to 30 min. The function of tonic calling might be an adaptation to predators that pose a longer threat (i.e. ambush predators) (Owings & Coss, 2007; Owings et al., 1986). In our study sites, feral cats are the terrestrial predators that hide in ambush and pose a persisting threat. A long repeated bark may also be necessary to determine whether another squirrel has actually seen a threat (Sloan & Hare, 2004), or reflect the arousal state of the caller (Briefer, 2012; Price & Fischer, 2014). Producing repeated alarm calls during or continuing after a threat (i.e. tonic calling) seems counter-intuitive, as tonic calls are the most demanding calls in terms of energy (Owings & Coss, 2007) and can be costly in terms of fitness (Sherman, 1977). However, we never observed a successful predator attack on a caller, suggesting that mortality costs associated with calling are low in Barbary ground squirrels.

Concluding Remarks and Future Studies

Our results suggest that the dilution of predation risk does not explain grouping in Barbary ground squirrels, because individual vigilance did not decrease with increasing group size. Collective detection of predators is partly supported, because collective vigilance increased with increasing group size and alarm calling is important in this species. Alarm calls convey information about predation risk but can also serve as an association between call and reflex alertness, or as a recruitment tool. Barbary ground squirrels perform low-quality vigilance but spend a greater proportion of their time being exclusively vigilant from raised positions, indicating that natural selection favours high-quality vigilance. Future research on vigilance in the Barbary ground squirrel could record all

behaviours of the individuals in sight to gain complete information on an individual's or a group's activity budget, or to test whether vigilance is dependent, i.e. either synchronized or coordinated, which may also explain the partial lack of a relationship between vigilance and group size in this species. In future studies a smaller radius could be used to define a group for two reasons. First, Barbary ground squirrels may not perceive individuals further away to be in the same group. Second, larger distances between alarm call signallers and receivers would make collective detection less effective (Beauchamp, 2015a; Fernández-Juricic, Beauchamp, & Bastain, 2007). This latter point is especially important since a greater distance between signaller and receiver results in lower predation risk perception for the receiver (Ducheminsky et al., 2014; Wheeler, 2010). Finally, a major question still remains: which individuals and groups are at the extremes (i.e. 0.2 and 0.8 quantile) of the vigilance levels? Social network analysis may prove useful to answer this question. Overall, our results show that collective detection is one of the benefits of grouping in the Barbary ground squirrel.

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References

- Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Systematic Ecology*, 5, 325–383.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227–267.
- Beauchamp, G. (2013). Is the magnitude of the group-size effect on vigilance underestimated? *Animal Behaviour*, 85, 281–285. <http://doi.org/10.1093/beheco/arn096>.
- Beauchamp, G. (2015a). Animal vigilance and group size: Theory. In *Animal vigilance: Monitoring predators and competitors* (pp. 117–139). London, U.K.: Elsevier Academic Press. <http://doi.org/10.1016/B978-0-12-801983-2/00005-X>.
- Beauchamp, G. (2015b). Synchronization and coordination of animal vigilance. In *Animal vigilance: Monitoring predators and competitors* (pp. 155–172). London, U.K.: Elsevier Academic Press.
- Beauchamp, G. (2017). Disentangling the various mechanisms that account for the decline in vigilance with group size. *Behavioural Processes*, 136, 59–63. <http://doi.org/10.1016/j.beproc.2017.01.014>.
- Beauchamp, G., & Ruxton, G. D. (2008). Disentangling risk dilution and collective detection in the antipredator vigilance of semipalmated sandpipers in flocks. *Animal Behaviour*, 75, 1837–1842. <http://doi.org/10.1016/j.anbehav.2007.12.016>.
- Bednekoff, P. A., & Lima, S. L. (1998). Re-examining safety in numbers: Interactions between risk dilution and collective detection depend upon predator targeting behaviour. *Proceedings of the Royal Society B: Biological Sciences*, 265(1409), 2021–2026. <http://doi.org/10.1098/rspb.1998.0535>.
- Bekoff, M. (1995). Vigilance, flock size, and flock geometry: Information gathering by western evening grosbeaks (Aves, Fringillidae). *Ethology*, 99(1–2), 150–161. <https://doi.org/10.1111/j.1439-0310.1995.tb01096.x>.
- Bell, M. B. V., Radford, A. N., Rose, R., Waide, H. M., & Ridley, A. R. (2009). The value of constant surveillance in a risky environment. *Proceedings of the Royal Society B: Biological Sciences*, 276(1669), 2997–3005. <http://doi.org/10.1098/rspb.2009.0276>.
- Bertram, B. C. R. (1978). Living in groups: Predators and prey. In J. R. Krebs, & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (pp. 64–96). Oxford, U.K.: Blackwell Scientific.
- Bertram, B. C. R. (1980). Vigilance and group size in ostriches. *Animal Behaviour*, 28, 278–286. [http://doi.org/10.1016/S0003-3472\(80\)80030-3](http://doi.org/10.1016/S0003-3472(80)80030-3).
- Blumstein, D. T. (2007). The evolution of alarm communication in rodents: Structure, function, and the puzzle of apparently altruistic calling. In J. O. Wolff, & P. W. Sherman (Eds.), *Rodent societies: An ecological & evolutionary perspective* (pp. 317–327). Chicago, IL: The University of Chicago Press.
- Blumstein, D. T., Barrow, L., & Luterra, M. (2008). Olfactory predator discrimination in yellow-bellied marmots. *Ethology*, 114(11), 1135–1143. <http://doi.org/10.1111/j.1439-0310.2008.01563.x>.
- Blumstein, D. T., & Daniel, J. C. (2003). Red kangaroos (*Macropus rufus*) receive an antipredator benefit from aggregation. *Acta Ethologica*, 5, 95–99. <http://doi.org/10.1007/s10211-002-0070-5>.
- Blumstein, D. T., Daniel, J. C., & Evans, C. S. (2001). Yellow-footed rock-wallaby group size effects reflect a trade-off. *Ethology*, 107, 655–664.
- Blumstein, D. T., Verneyre, L., & Daniel, J. C. (2004). Reliability and the adaptive utility of discrimination among alarm callers. *Proceedings of the Royal Society B: Biological Sciences*, 271(1550), 1851–1857. <http://doi.org/10.1098/rspb.2004.2808>.
- Bolker, B., Skaug, H., Magnusson, A., & Nielsen, A. (2012). Getting started with the glmmADMB package (R Package Version 2.0–8, 12). <http://glmmadmb.r-forge-project.org/glmmADMB.html>.
- Bradbury, J., & Vehrencamp, S. L. (1998). *Principles of animal communication*. Sunderland, MA: Sinauer.
- Briefer, E. F. (2012). Vocal expression of emotions in mammals: Mechanisms of production and evidence. *Journal of Zoology*, 288(1), 1–20. <http://doi.org/10.1111/j.1469-7998.2012.00920.x>.
- Brown, J., Laundre, W., & Gurung, M. (1999). The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, 80(2), 385–399.
- Cade, B. S., & Noon, B. R. (2003). A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, 1(8), 412–420. <http://doi.org/10.2307/3868138>.
- Cade, B. S., Noon, B. R., & Flather, C. H. (2005). Quantile regression reveals hidden bias and uncertainty in habitat models. *Ecology*, 86(3), 786–800. <http://doi.org/10.1890/04-0785>.
- Cade, B. S., Terrell, J. W., & Schroeder, R. L. (1999). Estimating effects of limiting factors with regression. *Ecology*, 80(1), 311–323.
- Catterall, C. P., Elgar, M. A., & Kikkawa, J. (1992). Vigilance does not covary with group-size in an island population of silvereyes (*Zosterops lateralis*). *Behavioral Ecology*, 3(3), 207–210. <http://doi.org/10.1093/beheco/3.3.207>.
- Chamaillé-Jammes, S., & Blumstein, D. T. (2012). A case for quantile regression in behavioral ecology: Getting more out of flight initiation distance data. *Behavioral Ecology and Sociobiology*, 66(6), 985–992. <http://doi.org/10.1007/s00265-012-1354-z>.
- Courter, J. R., & Ritchison, G. (2010). Alarm calls of tufted titmice convey information about predator size and threat. *Behavioral Ecology*, 21, 936–942. <http://doi.org/10.1093/beheco/arq086>.
- Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, 20(4), 187–193. <http://doi.org/10.1016/j.tree.2005.01.010>.
- Dall, S. R. X., Kotler, B. P., & Bouskila, A. (2001). Attention, 'apprehension' and gerbils searching in patches. *Annales Zoologici Fennici*, 38, 15–23.
- Dehn, M. M. (1990). Vigilance for predators: Detection and dilution effects. *Behavioral Ecology and Sociobiology*, 26(5), 337–342. <http://doi.org/10.1007/BF00171099>.
- Ducheminsky, N., Henzi, S. P., & Barrett, L. (2014). Responses of vervet monkeys in large troops to terrestrial and aerial predator alarm calls. *Behavioral Ecology*, 25, 1474–1484. <http://doi.org/10.1093/beheco/aru151>.
- Ebensperger, L. A., Hurtado, M. J., & Ramos-Jiliberto, R. (2006). Vigilance and collective detection of predators in degus (*Octodon degus*). *Ethology*, 112(9), 879–887. <http://doi.org/10.1111/j.1439-0310.2006.01242.x>.
- Edwards, S., & Waterman, J. M. (2011). Vigilance and grouping in the southern African ground squirrel (*Xerus inauris*). *African Journal of Ecology*, 49(3), 286–291. <http://doi.org/10.1111/j.1365-2028.2011.01262.x>.
- Elgar, M. (1989). Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biological Reviews*, 64(1), 13–33. <http://doi.org/10.1111/j.1469-185X.1989.tb00636.x>.
- Fairbanks, B., & Dobson, F. S. (2007). Mechanisms of the group-size effect on vigilance in Columbian ground squirrels: Dilution versus detection. *Animal Behaviour*, 73, 115–123. <http://doi.org/10.1016/j.anbehav.2006.07.002>.
- Favreau, F.-R., Goldizen, A. W., & Pays, O. (2010). Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. *Proceedings of the Royal Society B: Biological Sciences*, 277(1690), 2089–2095. <http://doi.org/10.1098/rspb.2009.2337>.
- Favreau, F.-R., Pays, O., Fritz, H., Goulard, M., Best, E. C., & Goldizen, A. W. (2015). Predators, food and social context shape the types of vigilance exhibited by kangaroos. *Animal Behaviour*, 99, 109–121. <http://doi.org/10.1016/j.anbehav.2014.11.001>.
- Fernández-Juricic, E., Beauchamp, G., & Bastain, B. (2007). Group-size and distance-to-neighbour effects on feeding and vigilance in brown-headed cowbirds. *Animal Behaviour*, 73, 771–778. <http://doi.org/10.1016/j.anbehav.2006.09.014>.

- Fernández, G. J., Capurro, A. F., & Rebores, J. C. (2003). Effect of group size on individual and collective vigilance in greater rheas. *Ethology*, 109(5), 413–425. <http://doi.org/10.1046/j.1439-0310.2003.00887.x>.
- Fernández-Juricic, E., Smith, R., & Kacelnik, A. (2005). Increasing the costs of conspecific scanning in socially foraging starlings affects vigilance and foraging behaviour. *Animal Behaviour*, 69, 73–81. <https://doi.org/10.1016/j.anbehav.2004.01.019>.
- Fortin, D., Boyce, M. S., & Merrill, E. H. (2004). Multi-tasking by mammalian herbivores: Overlapping processes during foraging. *Ecology*, 85(8), 2312–2322. <http://doi.org/10.1890/03-0485>.
- Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N., et al. (2012). AD model builder: Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, 27(2), 233–249. <http://doi.org/10.1080/10556788.2011.597854>.
- Furrer, R. D., & Manser, M. B. (2009). The evolution of urgency based and functionally referential alarm calls in ground dwelling species. *American Naturalist*, 173(3), 400–410. <http://doi.org/10.1086/596541>.
- Geraci, M. (2014). Linear quantile mixed models: The lqmm package for Laplace quantile regression. *Journal of Statistical Software*, 57(13), 1–29. <http://doi.org/https://doi.org/10.18637/jss.v057.i13>.
- Gouat, P., & Yahyaoui, I.-E. (2001). Reproductive period and group structure variety in the Barbary ground squirrel *Atlantoxerus getulus*: Preliminary results. In C. Denys, L. Granjon, & A. Poulet (Eds.), *African small mammals* (pp. 343–352). Paris, France: IRD Editions.
- Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, 31(2), 295–311. [http://doi.org/10.1016/0022-5193\(71\)90189-5](http://doi.org/10.1016/0022-5193(71)90189-5).
- Harris, M. A., Murie, J. O., & Duncan, J. A. (1983). Responses of Columbian ground squirrels to playback of recorded calls. *Zeitschrift für Tierpsychologie*, 63(4), 318–330. <http://doi.org/10.1111/j.1439-0310.1983.tb00747.x>.
- Hayes, A. R., & Huntly, N. J. (2005). Effects of wind on the behavior and call transmission of pikas (*Ochotona princeps*). *Journal of Mammalogy*, 86(5), 974–981. [http://doi.org/10.1664/1545-1542\(2005\)86\[974:EOWOTB\]2.0.CO;2](http://doi.org/10.1664/1545-1542(2005)86[974:EOWOTB]2.0.CO;2).
- Hirschler, I. M., Gedert, J. L., Majors, J., Townsend, T., & Hoogland, J. L. (2016). What is the best way to estimate vigilance? A comparison of two methods for Gunnison's prairie dogs, *Cynomys gunnisoni*. *Animal Behaviour*, 121, 117–122. <http://doi.org/10.1016/j.anbehav.2016.09.003>.
- Hochberg, Y. (1988). A sharper Bonferroni procedure for multiple tests of significance. *Biometrika*, 75(4), 800–802.
- Kildaw, S. D. (1995). The effect of group size manipulations on the foraging behavior of black-tailed prairie dogs. *Behavioral Ecology*, 6(4), 353–358. <http://doi.org/10.1093/beheco/6.4.353>.
- Klump, G. M., & Shalter, M. D. (1984). Acoustic behaviour of birds and mammals in the predator context I. Factors affecting the structure of alarm signals II. The functional significance and evolution of alarm signals. *Zeitschrift für Tierpsychologie*, 66, 189–226.
- Koprowski, J. L. (2002). Handling tree squirrels with a safe and efficient restraint. *Wildlife Society Bulletin*, 30(1), 101–103.
- Korstjens, A. H., Lehmann, J., & Dunbar, R. I. M. (2010). Resting time as an ecological constraint on primate biogeography. *Animal Behaviour*, 79, 361–374. <http://doi.org/10.1016/j.anbehav.2009.11.012>.
- Kotler, B. P., Brown, J. S., Dall, S. R. X., Gresser, S., Ganey, D., & Bouskila, A. (2002). Foraging games between gerbils and their predators: Temporal dynamics of resource depletion and apprehension in gerbils. *Evolutionary Ecology Research*, 4, 495–518.
- Lazarus, J., & Lazarus, J. (1979). Flock size and behaviour in captive red-billed weaverbirds (*Quelea quelea*): Implications for social facilitation and the functions of flocking. *Behaviour*, 71(1–2), 127–144. <http://doi.org/10.1163/156853979X00133>.
- Li, C., Beauchamp, G., Wang, Z., & Cui, P. (2016). Collective vigilance in the wintering hooded crane: The role of flock size and anthropogenic disturbances in a human-dominated landscape. *Ethology*, 122(12), 999–1008. <http://doi.org/10.1111/eth.12570>.
- Li, C., Jiang, Z., Li, L., Li, Z., Fang, H., Li, C., et al. (2012). Effects of reproductive status, social rank, sex and group size on vigilance patterns in Przewalski's gazelle. *PLoS One*, 7(2), 1–7. <http://doi.org/10.1371/journal.pone.0032607>.
- Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: The group-size effect. *Animal Behaviour*, 49, 11–20. [http://doi.org/10.1016/0003-3472\(95\)80149-9](http://doi.org/10.1016/0003-3472(95)80149-9).
- Lima, S. L., & Bednekoff, P. A. (1999). Back to the basics of antipredatory vigilance: Can nonvigilant animals detect attack? *Animal Behaviour*, 58, 537–543. <http://doi.org/10.1006/anbe.1999.1182>.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68, 619–640.
- López-Darias, M., & Lobo, J. M. (2008). Factors affecting invasive species abundance: The Barbary ground squirrel on Fuerteventura Island, Spain. *Zoological Studies*, 47(3), 268–281.
- Lung, M. A., & Childress, M. J. (2007). The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. *Behavioral Ecology*, 18(1), 12–20. <http://doi.org/10.1093/beheco/arl066>.
- Macedonia, J. M. (1990). What is communicated in the antipredator calls of lemurs: Evidence from playback experiments with ringtailed and ruffed lemurs. *Ethology*, 86(3), 177–190.
- Macedonia, J. M., & Evans, C. S. (1993). Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, 93, 177–197.
- Machado, A. (1979). The introduction of the Getulian squirrel (*Atlantoxerus getulus* L., 1758) in Fuerteventura, Canary Islands. *Egyptian Journal for Wildlife & Natural Resources*, 2, 182–202.
- Machado, A., & Domínguez, F. (1982). *Estudio sobre la presencia de la ardilla moruna (Atlantoxerus getulus L.) en la isla de Fuerteventura: Su introducción, su biología y su impacto en el medio*. Santa Cruz de Tenerife, Spain: Ministerio de Agricultura, Pesca y Alimentación, Instituto Nacional para la Conservación de la Naturaleza.
- Makenbach, S. A., Waterman, J. M., & Roth, J. D. (2013). Predator detection and dilution as benefits of associations between yellow mongooses and Cape ground squirrels. *Behavioral Ecology and Sociobiology*, 67(7), 1187–1194. <http://doi.org/10.1007/s00265-013-1544-3>.
- Manser, M. B. (1999). Response of foraging group members to sentinel calls in suricates, *Suricata suricatta*. *Proceedings of the Royal Society B: Biological Sciences*, 266(1423), 1013–1019. <http://doi.org/10.1098/rspb.1999.0737>.
- Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society B: Biological Sciences*, 268(1483), 2315–2324. <http://doi.org/10.1098/rspb.2001.1773>.
- Marzol Jaén, M. V. (1988). *La lluvia: Un recurso natural para Canarias*. Santa Cruz de Tenerife, Spain: Caja General de Ahorros de Canarias.
- McDonald, M., & Johnson, S. (2014). 'There's an app for that': A new program for the collection of behavioural field data. *Animal Behaviour*, 95, 81–87. <http://doi.org/10.1016/j.anbehav.2014.06.009>.
- McNamara, J. M., & Houston, A. I. (1992). Evolutionary stable levels of vigilance as a function of group size. *Animal Behaviour*, 43, 641–658.
- Medina, F. M., López-Darias, M., Nogales, M., & García, R. (2008). Food habits of feral cats (*Felis silvestris catus* L.) in insular semiarid environments (Fuerteventura, Canary Islands). *Wildlife Research*, 35(2), 162–169. <http://doi.org/10.1071/WR07108>.
- Melchior, H. R., & Iwen, F. A. (1965). Trapping, restraining, and marking Arctic ground squirrels for behavioral observations. *Journal of Wildlife Management*, 29(4), 671–678.
- Michelena, P., & Deneubourg, J. L. (2011). How group size affects vigilance dynamics and time allocation patterns: The key role of imitation and tempo. *PLoS One*, 6(4). <http://doi.org/10.1371/journal.pone.0018631>.
- Owings, D. H., & Coss, R. G. (1977). Snake mobbing by California ground squirrels: Adaptive variation and ontogeny. *Behaviour*, 62(1), 50–69.
- Owings, D. H., & Coss, R. G. (2007). Social and antipredator systems: Intertwining links in multiple time frames. In J. O. Wolff, & P. W. Sherman (Eds.), *Rodent societies: An ecological & evolutionary perspective* (pp. 305–316). Chicago, IL: The University of Chicago Press.
- Owings, D. H., Hennessy, D. F., Leger, D. W., & Gladney, A. B. (1986). Different functions of 'alarm' calling for different time scales: A preliminary report on ground squirrels. *Behaviour*, 99(1/2), 101–116.
- Pays, O., Dubot, A. L., Jarman, P. J., Loisel, P., & Goldizen, A. W. (2009). Vigilance and its synchrony in the red-necked pademelon, *Thylogale thetis*. *Behavioral Ecology*, 20(1), 22–29. <http://doi.org/10.1093/beheco/arm110>.
- Pays, O., Jarman, P. J., Loisel, P., & Gerard, J. F. (2007a). Coordination, independence or synchronization of individual vigilance in the eastern grey kangaroo? *Animal Behaviour*, 73, 595–604. <http://doi.org/10.1016/j.anbehav.2006.06.007>.
- Pays, O., Renaud, P. C., Loisel, P., Petit, M., Gerard, J. F., & Jarman, P. J. (2007b). Prey synchronize their vigilant behaviour with other group members. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1287–1291. <http://doi.org/10.1098/rspb.2006.0204>.
- Pays, O., Sirot, E., & Fritz, H. (2012). Collective vigilance in the greater kudu: Towards a better understanding of synchronization patterns. *Ethology*, 118(1), 1–9. <http://doi.org/10.1111/j.1439-0310.2011.01974.x>.
- Phillips, M. A., & Waterman, J. M. (2013). Olfactory snake-predator discrimination in the Cape ground squirrel. *Ethology*, 119(4), 278–285. <http://doi.org/10.1111/eth.12059>.
- Podgórski, T., de Jong, S., Bubnicki, J. W., Kuijper, D. P. J., Churski, M., & Jedrzejewska, B. (2016). Drivers of synchronized vigilance in wild boar groups. *Behavioral Ecology*, 27(4), 1097–1103. <http://doi.org/10.1093/beheco/aru016>.
- Price, T., & Fischer, J. (2014). Meaning attribution in the West African green monkey: Influence of call type and context. *Animal Cognition*, 17, 277–286. <http://doi.org/10.1007/s10071-013-0660-9>.
- Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology*, 38, 419–422.
- Quenette, P.-Y., & Gerard, J.-F. (1992). From individual to collective vigilance in wild boar (*Sus scrofa*). *Canadian Journal of Zoology*, 70(8), 1632–1635. <http://doi.org/10.1139/z92-226>.
- R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.r-project.org/>.
- Rieucou, G., Blanchard, P., Martin, J. G. A., Favreau, F.-R., Goldizen, A. W., & Pays, O. (2012). Investigating differences in vigilance tactic use within and between the sexes in eastern grey kangaroos. *PLoS One*, 7(9), e44801. <http://doi.org/10.1371/journal.pone.0044801>.
- Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal Behaviour*, 51, 1077–1086.

- Sherman, P. W. (1977). Nepotism and the evolution of alarm calls. *Science*, 197(4310), 1246–1253.
- Siro, E., & Touzalin, F. (2009). Coordination and synchronization of vigilance in groups of prey: The role of collective detection and predators' preference for stragglers. *American Naturalist*, 173(1), 47–59. <http://doi.org/10.1086/593358>.
- Sloan, J. L., & Hare, J. F. (2004). Monotony and the information content of Richardson's ground squirrel (*Spermophilus richardsonii*) repeated calls: Tonic communication or signal certainty? *Ethology*, 110(2), 147–156. <http://doi.org/10.1111/j.1439-0310.2003.00955.x>.
- Sloan, J. L., & Hare, J. F. (2008). The more the scarier: Adult Richardson's ground squirrels (*Spermophilus richardsonii*) assess response urgency via the number of alarm signalers. *Ethology*, 114(5), 436–443. <http://doi.org/10.1111/j.1439-0310.2008.01479.x>.
- Stankowich, T. (2003). Marginal predation methodologies and the importance of predator preferences. *Animal Behaviour*, 66, 589–599. <http://doi.org/10.1006/anbe.2003.2232>.
- Treves, A., Drescher, A., & Ingrisano, N. (2001). Vigilance and aggregation in black howler monkeys (*Alouatta pigra*). *Behavioral Ecology and Sociobiology*, 50(1), 90–95. <http://doi.org/10.1007/s002650100328>.
- Unck, C. E., Waterman, J. M., Verburg, L., & Bateman, P. W. (2009). Quantity versus quality: How does level of predation threat affect Cape ground squirrel vigilance? *Animal Behaviour*, 78, 625–632. <http://doi.org/10.1016/j.anbehav.2009.05.028>.
- Valone, T. J. (1989). Group foraging, public information, and patch estimation. *Oikos*, 56(3), 357–363.
- Waring, G. H. (1966). Sounds and communications of the yellow-bellied marmot (*Marmota flaviventris*). *Animal Behaviour*, 14, 177–183. [https://doi.org/10.1016/S0003-3472\(66\)80028-3](https://doi.org/10.1016/S0003-3472(66)80028-3).
- Warkentin, K. J., Keeley, A. T. H., & Hare, J. F. (2001). Repetitive calls of juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) communicate response urgency. *Canadian Journal of Zoology*, 79(4), 569–573. <https://doi.org/10.1139/cjz-79-4-569>.
- Waterman, J. M. (1995). The social organization of the Cape ground squirrel (*Xerus inauris*; Rodentia: Sciuridae). *Ethology*, 101(101), 130–147.
- Waterman, J. M. (1997). Why do male Cape ground squirrels live in groups? *Animal Behaviour*, 53, 809–817.
- Wheeler, B. C. (2010). Production and perception of situationally variable alarm calls in wild tufted capuchin monkeys (*Cebus apella nigratus*). *Behavioral Ecology and Sociobiology*, 64, 989–1000. <http://doi.org/10.1007/s00265-010-0914-3>.
- Whiteside, M. A., Langley, E. J. G., & Madden, J. R. (2016). Males and females differentially adjust vigilance levels as group size increases: Effect on optimal group size. *Animal Behaviour*, 118, 11–18. <http://doi.org/10.1016/j.anbehav.2016.04.025>.
- Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. New York, NY: Springer-Verlag. Retrieved from <http://ggplot2.org>.
- Ylönen, H., & Brown, J. S. (2007). Fear and the foraging, breeding and sociality of rodents. In J. O. Wolff, & P. W. Sherman (Eds.), *Rodent societies: An ecological & evolutionary perspective* (pp. 328–341). Chicago, IL: The University of Chicago Press.

Appendix

Table A1

Number of trapped and marked adult, subadult and juvenile Barbary ground squirrels per site from 2014 until 2016 on the island of Fuerteventura, Canary Islands, Spain (28°34'60"N, 13°58'0"W)

	Site	1			2			3		
	Year	2014	2015	2016	2014	2015	2016	2014	2015	2016
Males										
Adults		9	14	16	10	24	24	13	14	15
Subadults		4	0	0	4	0	0	0	0	1
Juveniles		8	36	29	22	40	32	5	37	27
Females										
Adults		8	20	25	19	29	38	13	20	19
Subadults		2	0	0	2	0	0	2	0	0
Juveniles		9	27	22	26	21	45	5	25	25
Total adults + subadults		23	34	41	35	61	62	28	34	35

Table A2

Summary statistics of our observation periods per site on Fuerteventura, Canary Islands, Spain

	\bar{X}	SD	Min.	Max.	N
Site 1	114.7	73.4	10	360	161
Site 2	83	64.3	10	400	183
Site 3	65.5	52.6	10	210	86

We provide the mean (\bar{X}), standard deviation (SD), minimum (Min.) and maximum (Max.) of the periods that we observed Barbary ground squirrels, in minutes, and the number of observation periods (N).