Synchronizing vigilance or taking turns as sentinels? The importance of testing assumptions

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Abstract

Coordinated behavior, such as hunting in lions and coordinated vigilance as antipredator behavior, are examples of benefits of group-living. Instead of asynchronous vigilance, some social species synchronize their vigilance bouts or take turns acting as sentinels. A sentinel system assumes that sentinels are located at raised positions, produce alarm signals when detecting danger, and alternate vigilance bouts. However, despite the importance of sentinel systems in understanding anti-predator behavior, many species with a described sentinel system have not been tested yet for the assumption of taking turns. To increase our knowledge on the evolution of vigilance behavior, we studied whether vigilance is coordinated in Barbary ground squirrels, *Atlantoxerus getulus*. We show that vigilance was coordinated but synchronized instead of taking turns. In this case, synchronized vigilance may be 1) an optimal activity when in good body condition (low costs), and, 2) an adaptation to anthropogenically altered habitats (large benefits). We demonstrate that synchronized vigilance may have greater fitness benefits than sentinel behavior in habitats where the field of view is obstructed by man-made structures and individuals must watch each other's backs for terrestrial predators. We conclude that it is essential to test assumptions of coordination and, thus, to analyze coordination to describe sentinel systems.

Keywords: anti-predator behavior, collective behavior, coordinated vigilance, invasive species, mammals

Significance Statement

Vigilance behavior can be vital to an animal's survival. A long-standing assumption of vigilance in social species is that vigilance bouts are independent among group members; but that does not always hold, as some species can coordinate their vigilance. Coordination of vigilance, either by taking turns acting as sentinels or synchronizing vigilance bouts, reduces the cost of the trade-off between feeding and

predation risk. A sentinel system assumes that sentinels are vigilant from raised positions, warn group members of danger, and alternate vigilance bouts. However, the assumption of alternating vigilance bouts remains poorly tested. We tested this assumption in invasive Barbary ground squirrels. We found that instead of alternating, individuals synchronized their vigilance bouts. Barbary ground squirrels may synchronize their vigilance 1) as an optimal activity when in good body condition, and, 2) to watch each other's back.

Introduction

Vigilance is essential for diurnal species to avoid predation resulting in a trade-off with foraging (Bednekoff and Lima 1998). Individuals are expected to balance the trade-off to increase their survival chances. In diurnal prey species, the cost of vigilance (less time available for foraging) can be reduced by performing nonexclusive or low-quality vigilance, i.e., individuals are vigilant while performing another behavior (e.g. Cape ground squirrels, *Xerus inauris,* Unck et al. (2009), or eastern grey kangaroos, *Macropus giganteus,* Favreau et al. (2015)). Low-quality vigilance is often seen in habitats where the risk imposed by predators is relatively low (Unck et al. 2009; Périquet et al. 2012). In riskier habitats, individuals increase their time spent in exclusive or high-quality vigilance –vigilance without performing any other behavior– while reducing the time spent foraging (Unck et al. 2009; Périquet et al. 2012). Thus, multi-tasking is one way to reduce the cost.

Another way to mitigate the foraging/vigilance trade-off cost is by coordinating vigilance. One long-standing assumption of vigilance models is that vigilance is independent among members of a social group, yet that does not always hold. Instead of independently scanning for predators, some species coordinate their vigilance (Beauchamp 2015). Following the definition of Pays et al. (2007a), coordination is considered as both taking turns acting as sentinels (nonoverlapping vigilance bouts) and synchronization of vigilance bouts (overlapping vigilance bouts). For example, individuals can be vigilant at the same time due to the same external stimulus (e.g., a predator, termed induced vigilance, Blanchard and Fritz 2007) or can be either vigilant or non-vigilant at the same time as other group members, resulting in overlapping vigilance bouts (Pays et al. 2007a; Beauchamp 2015). Synchronization of vigilance bouts is frequent both in birds and mammals (Ebensperger et al. 2006; Pays et al. 2007a, b, 2009, 2012; Öst and Tierala 2011; Podgórski et al. 2016; McDougall and Ruckstuhl 2018). In species with a sentinel system, one or two group members are always vigilant because individuals forego feeding and take turns performing high-quality vigilance from raised positions (Rasa 1987; Bednekoff 1997; Beauchamp 2015). Some highly social bird and mammal species living or foraging in open arid habitats perform sentinel behavior (Rasa 1977; Ferguson 1987; McGowan and Woolfenden 1989; Clutton-Brock

1999; Manser 1999; Wright et al. 2001; Newbold et al. 2008; Arbon et al. 2020). A sentinel system assumes that sentinels warn group members of danger (Bednekoff 1997) and that there is a continuous turn-over of who is sentinel, but there is no change in sentinel number (McGowan and Woolfenden 1989; Bednekoff 2015). Sentinels appear to be more effective at detecting predators due to their more focused vigilance and the elevated positions they adopt (Ridley et al. 2013). Nevertheless, sentinel behavior can be costly, as it is more likely to attract the attention of predators, e.g., dwarf mongoose, *Helogale parvula*, sentinels incur higher predation risk than non-sentinels (Ridley et al., 2013). Thus, coordination of guarding bouts may be a necessity to divide the costs of being on guard over group members. Since non-sentinels can be located at raised positions or can alarm signal, Bednekoff (2015) argued that the main criterion of a sentinel system is the alternation of the high-quality vigilance bouts. However, despite the importance of exploring the role of coordinated vigilance on species' survival, coordination was tested in only three species (meerkats, *Suricata suricatta,* superb fairy-wrens, *Malurus cyaneus*, and Florida scrub-jays, *Aphelocoma coerulescens*), and suggested for 14 species out of 40 species with a described sentinel system (Bednekoff 2015).

We used a population of Barbary ground squirrels, *Atlantoxerus getulus*, to show the importance of testing the assumptions of coordination in describing the vigilance behavior of diurnal prey species. *Atlantoxerus getulus* is an appropriate study system as both males and females perform high-quality vigilance (actively scan the environment without performing any other behavior for approximately 40% of their daily activity budget) (van der Marel et al. 2019). Barbary ground squirrels perform high-quality vigilance behaviors either on the ground or away from foraging areas in raised positions (>30 cm from the ground) (van der Marel, pers. obs.). We termed this latter vigilance type 'perch behavior'. Perch behavior seems similar to sentinel behavior as perched individuals are located at raised positions and alarm call to inform group members of danger (van der Marel et al. 2019). Thus, although Barbary ground squirrels meet two criteria of a sentinel system (van der Marel 2019; van der Marel et al. 2019), such behavior cannot be considered as sentinel behavior unless it is coordinated by individuals taking turns (following Bednekoff 2015). Our objectives are to investigate whether 1) perch behavior is costly; and, 2) Barbary

ground squirrels coordinate perch behavior either by taking turns acting as sentinels or by synchronization. First, we hypothesized that perch behavior is costly as individuals would have less time to forage, and thus are predicted to have a lower body condition, and a lower survival chance, mainly because perched individuals would attract the attention of predators (only perched when predators are present). Second, we hypothesized that Barbary ground squirrels coordinate perch behavior by taking turns acting as sentinels.

Materials and methods

Study sites, species, and trapping protocol

We studied an invasive population of Barbary ground squirrels in the northwest of Fuerteventura, Canary Islands, Spain (28°34'60" N, 13°58'0" W), from March through July 2014, January through July 2015, and January through June 2016. Fuerteventura has an arid climate and semi-desert habitats characterized by xerophytic scrubland and ravines caused by erosion (del Arco Aguilar et al. 2010). Dams and rock walls, built to make terraces for land cultivation and to fence properties, characterize island landscapes and also our field sites, and function as shelters and perches for the Barbary ground squirrels to watch for predators (López-Darias and Lobo 2008; van der Marel et al. 2019). The main predators of Barbary ground squirrels on Fuerteventura are the native Eurasian buzzard, *Buteo buteo* (Gangoso et al. 2006) and the invasive feral cat, *Felis catus*- the only terrestrial predator (Medina et al. 2008). Other occasional aerial predators are the common raven, *Corvus corax* (Gangoso et al. 2006) and the common kestrel, *Falco tinnunculus* (López-Darias and Lobo 2008). The study area consisted of three study sites on average 0.73 km apart from one another (Site 1: 283558.1N, 135949.15W; Site 2: 283536.81N, 13° 5948.71W; and Site 3: 283538.51N, 140001.41W). The sites differed in the number of squirrels and size (density of squirrels per hectare was 14.15, 9.19 and 7.24 for site 1, 2 and 3, respectively, van der Marel et al. 2019, 2020), but did not represent distinct squirrel populations (van der Marel et al. 2020). Over the three years, we sighted a total of 175 aerial and 96 terrestrial predators and the number of predator

sightings was similar across all three sites (van der Marel et al. 2019). We observed five successful (out of 10) aerial predator attacks and one successful (out of 4) terrestrial predator attacks (van der Marel et al. 2019). As the sites were close to one another and only differed in squirrel density, we decided not to include site as a random factor in any of our models.

As part of a broader research project, we continuously monitored the population of the study area by trapping Barbary ground squirrels weekly throughout the three field seasons following the procedures described in van der Marel et al. (2019, 2020, 2021) and Piquet et al. (2018). For unique identification, we PIT-tagged and gave each individual a unique dorsal dye mark. For this study, we additionally measured squirrel body mass using a spring scale (± 5 g; Pesola AG, Baar, Switzerland) and hindfoot length (mm) using a Digimatic Plastic Caliper (Mitutoyo Corporation, Kawasaki, Japan), both as proxy measurements for body size (Schulte-Hostedde et al. 2001).

Barbary ground squirrels are social because individuals share sleeping burrows and show spatiotemporal overlap and cohesiveness (van der Marel et al. 2020). Females are the philopatric sex and as such they share sleeping burrows with related adult females (1-8 females), whereas males disperse before sexual maturation and share sleeping burrows with unrelated males and subadults of either sex when they are present (1-16 individuals) (van der Marel et al. 2020). Female sleeping burrow group composition is more stable than for males; but throughout the day, males and females of different sleeping burrow associations can be active in the same area in a site, showing fission-fusion dynamics (van der Marel et al. 2020). Therefore for this study, we used two group definitions: as individuals sharing a sleeping burrow together and as a set of individuals that were in each other's visible range during an observation period (Stankowich 2003; van der Marel et al. 2019). We did not consider auditory range as part of our group definition as we heard alarm calls from different sites and we do not know at what distance squirrels can hear alarm calls. In our study area, the squirrels prefer small ravines with old lava tunnels that function as burrows or areas with rock walls that formed terraces for land cultivation (López-Darias and Lobo 2008; van der Marel et al. 2020).

We distinguished adult and subadult males and females by the state of their primary sexual characters

(scrotum or vulva and nipples, van der Marel et al. 2020a, 2021). Subadults are over six months old and have reached adult body size, but males do not have descended testes and females do not have swollen vulva and nipples during the mating season (i.e., days when females are in estrus). The mating season is distinct as males regress their scrotum once all females have mated (van der Marel et al. 2021). Males have been observed to travel between sites only during the mating season; otherwise, adult males and females of all ages stay within a site (van der Marel, pers. obs).

Behavioral observations

To characterize the perch behavior of Barbary ground squirrels, we used 10 min scan samples throughout each behavioral observation period (Altmann 1974). It was not possible to record data blind because our study involved focal animals in the field. We conducted behavioral observations during all three field seasons between 9:30 h GMT and 2 h before sunset, i.e., when the squirrels are active above ground (Machado 1979; van der Marel et al. 2019). We observed the squirrels within each site from elevated areas and roads at a distance of approximately 50 m, which did not affect the squirrels' behavior. The human observers that visited the sites were not perceived as a threat to the squirrels as the squirrels did not change their behavior when the observers arrived (van der Marel, pers. obs). Primarily, we recorded observed perch behavior, low-quality vigilance (vigilance at any location that lasted < 30 s or was performed while doing other behaviors), and feeding (actively searching for, manipulating, and/or ingesting a food item). We also recorded whether any predators or other external stimuli were observed in a scan, as animals may respond to the same external stimulus (Beauchamp et al. 2012; McDougall and Ruckstuhl 2018). To enter behavioral data, we used the spreadsheet program Numbers (Apple, Cupertino, CA, USA) on an iPod (Apple, Cupertino, CA, USA) from 2014 until June 2015, and thereafter Prim8 Software (McDonald and Johnson 2014) on an Android phone (Motorola Droid A850).

Statistical analyses

For all our analyses, we selected individuals that were observed for at least 50 min over a minimum of five observation periods (Edwards and Waterman 2011). We excluded days that females were in estrus (the mating season) because male behavior changed as they search competitively for estrous females, similar to Cape ground squirrels (Waterman 1998). We performed all analyses in R version 3.4.1 (R Core Team 2017) and we made the figures using "ggplot2" package version 3.0.0 (Wickham 2016). We set statistical significance to the level of 0.05. Unless otherwise indicated, we denote averages as mean ± standard error (SE).

General description of foraging and perch behavior

Using the scan data recorded across all three field seasons, we calculated the distance to foraging areas, the distance from cover while foraging, the number of squirrels foraging per scan, and the distance between foraging and perching group members. Using Google Earth, we calculated the distance from sleeping burrows to foraging areas and from foraging areas to cover (rock walls/burrows). For the distance between group members per scan, we excluded individuals that were out of sight and 33 observations with distances over 200 m as these observations were at the extremes at which we could confidently identify the squirrels. To investigate whether all individuals perform perch behavior, we calculated the percentage of individuals that perch from all marked individuals during the three field seasons. We analyzed whether the ground squirrels increase their perch behavior when predators were observed *vs.* when predators were not observed using a Mann-Whitney *U* test. If we saw an aerial predator in a scan, that complete scan was considered to have a predator. If we saw a terrestrial predator, we considered the complete observation session to have a predator, as cats are the ambush predators in our study sites.

Costs of perch behavior

We tested if any costs are associated with perch behavior using the full dataset (2014-2016). As independent variables, we used the proportion of time spent feeding, body condition and age at which the squirrels disappeared (survival age). We measured body condition by taking the residuals from a linear regression of log body mass (g) on log hind foot length (mm) (Labocha et al. 2014; Piquet et al. 2018). We calculated survival age as the age the squirrels lived until they disappeared (which entails death as the adult squirrels do not disperse from their site). Survival age may be an underestimate as we do not have the date of birth or the year the squirrels disappeared of all squirrels because our field season was only 3 years in duration. We tested for multicollinearity of our variables using the variance inflation factor (vif) function in the "car" package (Fox and Weisberg 2011). None of our variables showed a vif value above 3, so we included all variables. We used ID and year as random factors. We used glmmADMB (Bolker et al. 2012; Fournier et al. 2012) and the likelihood ratio test (LRT) from the 'lmtest' version 0.9-36 (Zeileis 2002) as the proportion of time spent perched followed a beta distribution.

Perch behavior coordination analyses

In our coordination analyses, we only used scan data recorded with the Prim8 software, as this software measured the exact duration of perch behavior instead of the number of times the behavior was observed. So, we excluded instances where perch events were shorter than 30 s. To measure coordination of perch bouts, we compared the observed proportion of time when at least one individual was perched per group with the expected proportion under the assumption of independent vigilance following the descriptions in, e.g., Pays et al. 2007a; Öst and Tierala 2011; Beauchamp 2015, which is the opposite from what is described in Bednekoff (2015). We measured the observed time as the total time spent perched divided by the total time observed for each individual in the group. We measured the expected time as $1 - \prod_{i=1}^{n}(1 - p_i)$, where n is the sample size and p_i is the proportion of time that individual i is perched, i.e., total time spent perched divided by the total time observed for that individual (Pays et al. 2007a; Öst and Tierala 2011; Beauchamp 2015). We calculated the duration of observed and expected

time when at least one individual was perched for all individuals, only adult individuals, and only adult females, excluding unidentified and unknown squirrels. We used two different sample size definitions: First, we used the number of observation periods as our sample size assuming that the individuals seen in an observation period belonged to the same group (see methods section *Behavioral observations*). Second, to prevent pseudoreplication, we used the number of social groups, which we defined as individuals sharing the same sleeping burrow (i.e., sleeping burrow associations). We used a non-parametric paired test (Wilcoxon signed-rank test with continuity correction) to test for differences between the expected and observed values per sample size. If the difference in proportions (p_{obs}-p_{exp}) did not differ from 0, then individual perch bouts were independent; if the difference in proportions was greater than 0, then perch bouts were sentinel; and if the difference was smaller than 0, then perch bouts were synchronized (Beauchamp 2015).

Results

General description of foraging and perch behavior

Upon emergence from their sleeping burrows in the morning (9:30-11:00), the ground squirrels were slow to wake-up, but eventually, all squirrels moved away from their sleeping burrow location to foraging areas and the last squirrels immerged in their burrows as early as 15:30 when it was cool and rainy and as late as 20:00 in the summer months (van der Marel, pers. obs). We observed 416 feeding and 1625 perch bouts in the morning (between 9:30 and 12:00), 360 and 1070 during midday (12:00-15:00) and 982 and 1928, respectively, in the afternoon (15:00 until immergence into the sleeping burrows, between 15:30 and 20:00). The maximum distance that squirrels moved from sleeping burrows to foraging areas was 185.5 ± 78.2 m (mean ± SD, n = 14) and the average distance to cover when foraging was 3.7 ± 3.1 m (mean ± SD) with a maximum distance of 20 m (n = 154 observations). The proportion of individuals feeding and perching in a 10-minute scan was 0.13 ± 0.22 (mean ± SD, n = 3131 scans) and 0.38 ± 0.33 (mean ± SD, n = 3131 scans), respectively, ranging from no individuals to all individuals performing the behavior. The distance between individuals that were observed in the same scan was 41.6

± 29.5 m (mean ± SD, n = 5418 observations), ranging from 0 to 197 m. Between individuals that belonged to the same sleeping burrow association, the distance was 36.9 ± 28.0 m (range: 0-187 m, n = 2656 observations). Per scan, the average distance was 23.1 ± 21.1 m (range: 0-139 m, n = 495) between foraging and 43.7 ± 29.5 m (range: 0-197 m, n = 1515) between perching individuals, respectively. When selecting for just individuals that share the same sleeping burrow, the average distance was 20.8 ± 20.5 m (range: 0-112 m, n = 248) for foraging and 38.5 ± 27.4 m (range: 0-183 m, n = 694) for perching individuals.

Overall, 99.3% of the squirrels (adults, subadults, and juveniles, n = 139) were observed perching. In 32.4% of a total of 3228 scans just one individual perched, while more than one squirrel was perched in 39.7% of scans. One individual perched in 32.9 % and more than one squirrel was perched in 38.4% scans of a total of 3018 scans when predators were not observed (Fig. 1a). When predators were observed, one squirrel was perched in 24.8% of scans and more than one squirrel in 59.5% of scans (n = 210 scans, Fig. 1a). Individuals perched both in the presence (0.46 ± 0.02, n = 210 scans) and absence of predators (0.38 ± 0.01, n = 3018 scans), although, the proportion of individuals perched per scan when a predator was observed was significantly higher than when no external stimulus was observed (Mann-Whitney *U* test: $U = 266581$, $P = 0.02$, effect size r = 0.07; Fig. 1b).

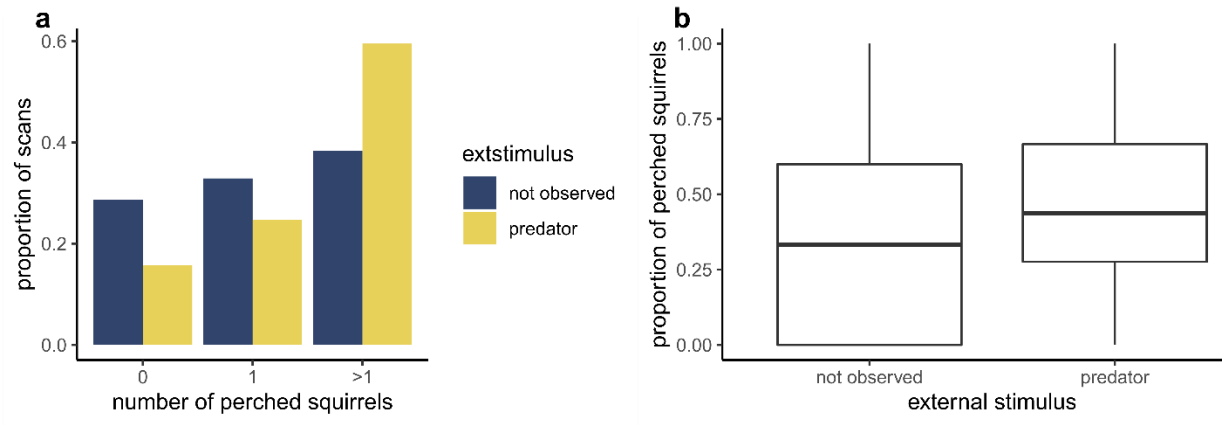

Figure 1. a) The proportion of scans where 0, 1, or more than 1 Barbary ground squirrels were perched when predators were and were not observed (controlled for number of scans), and b) the proportion of perched squirrels when predators were and were not observed.

Costs of perch behavior

We found that perch behavior can be costly (LRT, $\Lambda = 45.2$, $P < 0.001$; Fig. 2). Yet, although we found a negative relation between the amount of time spent perched and foraging (GLMM: -2.38 ± 0.42, random factors ID = 0.04 and year = 0.05, Fig. 2a), body condition was positively related to time spent perching (GLMM: 0.56 ± 0.19, Fig. 2b) and we did not find a relation between the proportion of time spent perched and survival age (GLMM: -0.03 ± 0.04, Fig. 2c).

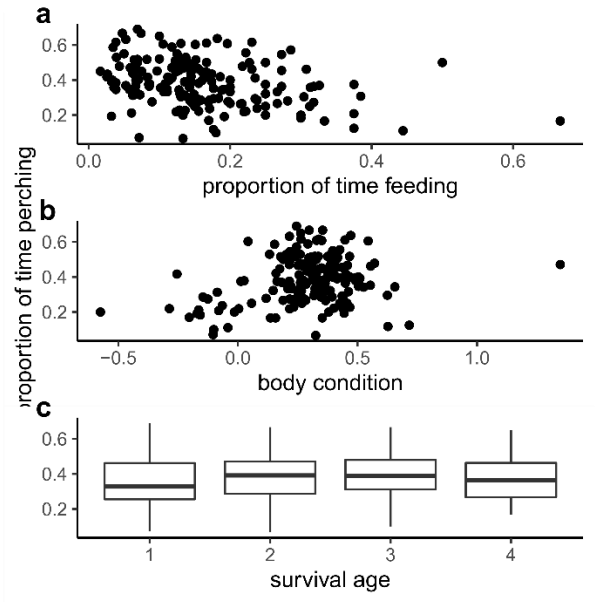

Figure 2. The relationship between the proportion of time perching and a) foraging, b) body condition, and c) survival age.

Perch behavior coordination analyses

We found that the proportion of observed time that at least one individual in the group (defined as either observation period or sleeping burrow association) was perched (p_{obs}) was smaller than the proportion of expected time (p_{exp}, Table 2). Furthermore, p_{obs}-p_{exp} was smaller than 0 for most groups (Table 2, Fig. 3).

Table 2 The proportion of observed (p_{obs}) and expected (p_{exp}) time at least one individual was perched (mean ± SE) per observation period in Barbary ground squirrels, calculated as duration of perch bouts

Sample	N	p_{obs}	p_{exp}	P_{obs}-P_{exp}	*V*	*P*
Observation session						
All individuals	119	0.17 ± 0.02	0.49 ± 0.03	-0.33 ± 0.03	123.5	<0.001
Adults	118	0.17 ± 0.02	0.49 ± 0.03	-0.32 ± 0.03	129.5	<0.001
Adult females	110	0.16 ± 0.01	0.39 ± 0.03	-0.28 ± 0.02	26.5	<0.001
Sleeping burrow associations						
Sleeping burrow associates	20	0.12 ± 0.02	0.37 ± 0.06	-0.25 ± 0.05	25	<0.001

Sample size (*N*) and the pairwise test results (*V* and *P*) are included.

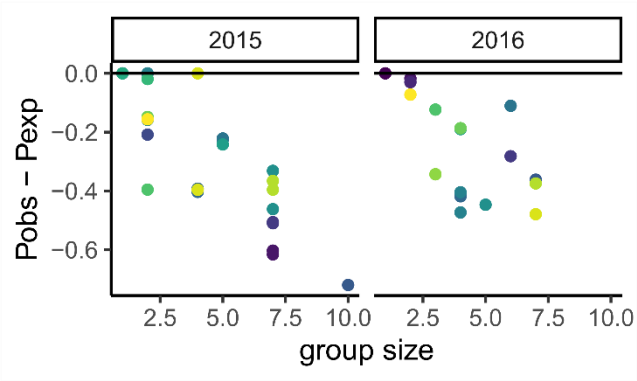

Figure 3. Difference between the observed (p_{obs}) and expected (p_{exp}) proportions of time when at least one Barbary ground squirrel was perched per group, defined as a sleeping burrow association. Each color represents a different social group. When the difference is smaller than 0, vigilance is synchronized.

Discussion

We studied whether perch behavior was costly and whether Barbary ground squirrels coordinate perch behavior either by taking turns acting as sentinels or by synchronization. Perch behavior cannot be considered induced vigilance (Blanchard and Fritz 2007) because perch behavior was performed in the absence and presence of an external stimulus (a predator). We found that perch behavior resulted in less time for foraging; however, the reduction in foraging time did not result in lower body condition or lower survival chances. Perch behavior was coordinated and synchronized in Barbary ground squirrels because the observed time that at least one individual is perched was smaller than the expected time, resulting in a difference in proportions smaller than zero. When testing the assumption of taking turns, the results may show that coordination of vigilance is absent altogether (Hing et al. 2019), synchronized (e.g., our study; Wang et al. 2020), or switches between synchronization and taking turns dependent on level of disturbance and predation risk (Kong et al. 2021). Using Barbary ground squirrels as a study species, we have been able to highlight the importance of testing assumptions to describe and understand vigilance behavior in diurnal prey species.

Since it seems counterintuitive to be on the lookout at the same time as your group members, the question is: why group members synchronize high-quality vigilance bouts? First, Barbary ground squirrels may have the time and energy to perform perch behavior, i.e., the costs of perch behavior are low. Although squirrels forage less when perching more, it does not result in lower body condition nor decreased survival chances. These results suggest that Barbary ground squirrels on Fuerteventura may be able to afford a reduction in foraging behavior due to the available resources or the release of enemies (parasites and predators) on the island compared to the native range (López-Darias 2007; López-Darias and Nogales 2008; Piquet et al. 2018). Normally, herbivores spend a great proportion of the time foraging to meet daily energy requirements (Fortin et al. 2004) and often rarely stop chewing (McDougall and Ruckstuhl 2018). But the mainly herbivorous Barbary ground squirrels spend a surprisingly small proportion of time foraging (12.8 ± 1.1%, van der Marel et al. 2019) in comparison to other species (52.0 ± 3.0% in Cape ground squirrels, Waterman, 1995; Unck et al. 2009; 87% in eastern grey kangaroos, Gélin et al. 2013; 64% in chestnut-crowned babblers, *Pomatostomus ruficeps*, Sorato et al. 2012; and 40% in Florida scrub-jays, *Aphelocoma coerulescens*, Fleischer Jr et al. 2003). Furthermore, although predators are present on Fuerteventura, predator diversity is lower in the invasive range (1 terrestrial and 3 aerial predators) compared to the native range (8 terrestrial and 2 aerial predators, Machado and Domínguez 1982). Also, individuals that are positioned at raised positions are more likely to attract the attention of predators and may incur higher predation risk (Ridley et al. 2013); Barbary ground squirrels perform more perch behavior when predators are present, but the effect size is small and perching does not result in lower survival in Barbary ground squirrels. The rock walls that are present on Fuerteventura provide not only better lookouts but also more shelter options for the squirrels. Thus, when Barbary ground squirrels are perched at elevated positions, the squirrels are closer to cover compared to when they are foraging. Overall, squirrels in good body condition may perform perch behavior as an optimal activity, which may imply that the trade-off between vigilance and feeding might be reduced in the invasive population of Barbary ground squirrels.

A second mechanism to explain synchronized vigilance is the presence of rock walls in the habitat. These rock walls prevent the squirrels from detecting terrestrial ambush predators when on the ground as they cannot look on either side of the wall. Visual cues are essential for predator detection in diurnal species and, thus, for ground-dwelling sciurids, whereby predator detection is easier in an open-structured habitat (Ylönen and Brown 2007; Embar et al. 2011). Hence, to adequately detect ambush predators, i.e., feral cats, two Barbary ground squirrels may be necessary to look in both directions of the rock wall, which is supported by the result that in the majority of scans more than 1 squirrel is perched. Synchronization of perch bouts may also explain our earlier result that individual high-quality vigilance sometimes increased with group size (van der Marel et al. 2019). In the stingless bee, *Tetragonisca angustula,* guards are present to defend the nest entrance and these guards are evenly distributed on either side of the entrance to increase the view of their surroundings (Shackleton et al. 2018). Therefore, similar to synchronized vigilance in bees, perch behavior may simply be a form of extremely exclusive vigilance where individuals improve their level of detection by synchronizing vigilance bouts to watch 'each other's back'. As such, perch behavior may function as a form of collective sentinel behavior, which requires further attention.

We found that perching behavior is much more synchronized than the calculated expectation. While other studies have reported some persistent synchronization of vigilance, the difference has often been small (Pays et al. 2007a, b, 2012; Öst and Tierala 2011; Podgórski et al. 2016; Wang et al. 2020). Some possible factors could have influenced our larger difference: as we used an observational study in the field, overall vigilance levels (Beauchamp 2015), distance between neighbors (Pays et al. 2009), group size (Beauchamp 2015), number of individuals out of sight, and other ecological reasons, e.g., rainfall, could have affected levels of synchronization. Furthermore, Barbary ground squirrels show fission-fusion dynamics (van der Marel et al. 2020), and therefore, the sample sizes that we used, observation period and sleeping burrow associations, may not be the optimal method to calculate coordination. Using observation period, we include all individuals in sight during a scan but this method may result in pseudoreplication as individuals can be observed on multiple days. Using sleeping burrow

associations, we prevent pseudoreplication but we exclude individuals that belonged to another sleeping burrow association even though they were observed in the same scan, resulting in lower confidence of coordination. However, using both these extremes, we still obtained the same result, suggesting that we captured the real coordination pattern of Barbary ground squirrels.

Conclusions

This study serves as an example of the importance of testing assumptions and shows that quantitative testing of coordination is essential to describe a sentinel system. In addition, we demonstrate that two non-mutually exclusive hypotheses may explain synchronization of perch bouts in the invasive population of Barbary ground squirrels: 1) squirrels have the time and energy to perform synchronized perch behavior (low cost), and, 2) the benefits are large in terms of evading ambush predators and scanning effectiveness (watch each other's back). Thus, coordinated vigilance behaviors may have evolved to reduce the foraging/vigilance trade-off and synchronized vigilance may result in fitness benefits, particularly, in habitats where the field of view is obstructed by man-made structures.

Declarations

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Ethics approval: All applicable international, national, and institutional guidelines for the care and use of animals were followed. All procedures performed were in accordance with the ethical standards of the institution or practice at which the studies were conducted (University of Manitoba Animal Care and Use Committee, protocol no. F14-032, and the government of Fuerteventura, Cabildo Insular de Fuerteventura no. 14885).

Availability of data and code: The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Authors' contributions: All authors conceived the ideas and designed methodology; AM collected the data, analyzed the data, and led the writing of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

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