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

Running title: Synchronized not sentinel high-quality vigilance

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Abstract

Diurnal species can reduce the cost of the trade-off between feeding and predation risk by 1) performing low-quality (vigilance while performing another behavior) instead of high-quality vigilance (only performing vigilance) or 2) by vigilance coordination either by taking turns acting as sentinels or by synchronizing vigilance bouts. A sentinel system assumes that sentinels are located at raised positions, alarm signal, and alternate vigilance bouts. However, many species with a described sentinel system have not been tested yet for coordination. We set out to study coordinated behavior and the reasons for this behavior in the invasive Barbary ground squirrel, *Atlantoxerus getulus*, using behavioral observations and genetic analyses. This species performs a type of vigilance (‘perch behavior') seemingly similar to sentinel behavior as individuals performed high-quality vigilance at raised locations for over 30 s, but alternating coordination is unknown. Perch behavior was coordinated but synchronized instead of taking turns (sentinel). Both sexes performed perch behavior and individuals performed perch behavior in the absence and presence of kin and offspring. We found that survival or time spent foraging did not decrease for perched individuals, nor that individual survival increased. Perch behavior in the invasive population of *A. getulus* may be synchronized 1) to perform an optimal activity when satiated (low costs), and, 2) may be an adaptation to habitat structure (large benefits). Our study demonstrates that the cost of the vigilance/foraging trade-off may not be high for invasive species and argued the importance of testing for coordination in species with described sentinel systems.

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

Introduction

Environmental conditions impose a notable investment in vigilance for diurnal species, as vigilance is required to avoid predation resulting in a trade-off with foraging(Bednekoff and Lima 1998). Thus, an individual will balance the trade-off to increase its survival chances. Different vigilance behaviors evolved due to the cost associated with this trade-off between vigilance and foraging. First, some species can reduce the cost of this trade-off 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. 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).

The cost of the trade-off between feeding activity and predator avoidance can additionally lead to the evolution of dependent vigilance within groups –individuals within the group coordinate the vigilance bouts– either by synchronizing their vigilance bouts or by taking turns acting as sentinels (Beauchamp 2015). Synchronization of vigilance bouts arises when individuals are either vigilant or non-vigilant at the same time as other group members, resulting in periods that either no group members or multiple group members are simultaneously vigilant (Beauchamp 2015). This behaviour, which is frequent in both birds and mammals (Ebensperger et al. 2006; Pays, Jarman, et al. 2007; Pays, Renaud, et al. 2007; Pays et al. 2009, 2012; Öst and Tierala 2011; Podgórski et al. 2016; McDougall and Ruckstuhl 2018), could occur through different mechanisms. First, vigilance levels of the group may convey the group's fear level

('contagion-of-fear' hypothesis, Sirot and Touzalin 2009; Beauchamp 2015), i.e., the level of fear is heightened when other group members experience many vigilant neighbors as an indication of potential predation risk (Beauchamp 2015). Second, synchronization can arise when individuals benefit by detecting predators and by reaching safety before group members, as predators target individuals that are last to find cover (‘predators-targeting-behavior’ hypothesis, Sirot and Touzalin 2009; Beauchamp 2015). Third, multiple guards may be necessary to increase the collective view of the surroundings (Shackleton et al. 2018). Additionally, synchronization may occur when individuals respond to a) the same external stimulus (e.g., a predator, termed induced vigilance, Blanchard and Fritz 2007), b) group members that ceased chewing (McDougall and Ruckstuhl 2018), or c) group members that started feeding (Beauchamp 2015). Thus, group members may simply be copying the behavior of nearest neighbors (Evans et al. 2018).

The foraging-vigilance trade-off can also lead to the evolution of sentinel behavior. 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, Berg, et al. 2001; Newbold et al. 2008). 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). 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. As alternating reduces the cost of the foraging and vigilance trade-off for group members. However,

out of 40 species with a described sentinel system, coordination was tested for only 3 species, although suggested for another 14 species (Bednekoff 2015). A sentinel system may evolve because sentinels appear to be more effective at detecting predators due to the more focused vigilance and the elevated positions they adopt (Ridley et al. 2013). Besides, sentinel behavior may be a cooperative behavior (Santema and Clutton-Brock 2013), where individuals gain fitness benefits through kin selection (sentinels only keep watch when close kin are present) or reciprocal altruism (Rasa 1987; McGowan and Woolfenden 1989; Brandl and Bellwood 2015). Nevertheless, sentinel behavior can be costly, as it is more likely to attract the attention of predators (Ridley et al. 2013). Consequently, coordination of guarding bouts may be a necessity to divide the costs of being on guard (increased predation risk and/or less time available for foraging) over group members (Ridley et al. 2013). Yet, sentinels may be considered selfish when they can detect a predator earlier and reach safety before group members or when the decision to become sentinel is state-dependent (Bednekoff 1997; Clutton-Brock 1999; Bednekoff 2001; Wright, Berg, et al. 2001; Wright, Maklakov, et al. 2001; Bednekoff and Woolfenden 2003). Most species with a sentinel system present stable social groups with high-relatedness among group members due to low levels of promiscuity (Fernández et al. 2003), suggesting that kin selection is an important mechanism for sentinel behavior to occur. However, other species are also sentinel when nonkin are nearby (Bednekoff and Woolfenden 2003). Thus, the role of kin selection in coordinated vigilance is not necessarily a prerequisite.

Besides environmental conditions, social conditions –sex, age and possibly kinship- may influence vigilance. For instance, due to intraspecific competition (Reboreda and Fernandez 1997) or mate protection (Horrocks and Hunte 1986) males are often the sex performing the most vigilance (Li et al. 2012; Pays et al. 2012; Whiteside et al. 2016). As well, adults normally

spend more time vigilant than juveniles (newborn sexually immature individuals that need more time feeding to maintain a high growth rate; Lung and Childress 2007; Pays et al. 2012). In some species kinship positively affects vigilance (Black and Owen 1989; Griesser 2003), although this pattern is not universal (Fairbanks and Dobson 2010; Quirici et al. 2013).

In the invasive population of Barbary ground squirrels, *Atlantoxerus getulus*, on Fuerteventura, Canary Islands, Spain, both males and females perform high-quality vigilance (actively scan the environment > 30 s without performing any other behavior for approximately 40% of their daily activity budget) while positioned on top of, mainly, man-made rock walls (van der Marel et al. 2019). We termed this particular vigilance behavior ‘perch behavior' because it is different from high-quality vigilance in that individuals move away from foraging areas to perform exclusive vigilance in a raised position (van der Marel et al. 2019). As well, perched individuals alarm call to inform group members of danger (van der Marel et al. 2019). Hence, perch behavior seems similar to sentinel behavior, although following Bednekoff (2015) such behavior cannot be considered as sentinel behavior unless it is coordinated by individuals taking turns. Thus, our main aim in this contribution is to deepen the understanding of factors explaining vigilance behavior in a social ground squirrel, which will aid in our comprehension of the evolution of coordinated vigilance in general. More specifically, our objectives are to investigate whether 1) Barbary ground squirrels coordinate perch behavior either by taking turns acting as sentinels or by synchronization, and are situated in higher positions when perched than when they are performing other behaviors; 2) perch behavior in this species is an induced vigilance; and, 3) social and environmental conditions -sex, age, kinship, resource availability or predation pressure- influence perch behavior using the hypotheses and predictions presented in Table 1.

Materials and methods

Study sites, species, and trapping protocol

We studied an invasive population of Barbary ground squirrels in the northwest of Fuerteventura, the 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. The study area consisted of three study sites that differed in the number of squirrels and size, but that did not represent distinct squirrel' populations (see van der Marel et al. 2020 for more details). 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 predator of Barbary ground squirrels on Fuerteventura is the Eurasian buzzard, *Buteo buteo* (Gangoso et al. 2006). Other aerial predators are the common raven, *Corvus corax* (Gangoso et al. 2006) and the common kestrel, *Falco tinnunculus* (López-Darias and Lobo 2008), whereas the invasive feral cat, *Felis catus*, is the only terrestrial predator (Medina et al. 2008).

Barbary ground squirrel is a social species because individuals share sleeping burrows and show spatiotemporal overlap and cohesiveness (van der Marel et al. 2020). Females share sleeping burrows with related adult females, whereas males share sleeping burrows with unrelated males and subadults of either sex when they are present. Throughout the day, males and females of different sleeping burrow associations can be active in the same area in a site (van der Marel et al. 2020). Adult and subadult males and females are distinguished by the

state of their primary sexual characters (scrotum or vulva and nipples, van der Marel et al. 2020). Subadults are over six months old, 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 mated (van der Marel 2019).

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. We followed the trapping and marking procedures described in van der Marel et al. (2019, 2020) and Piquet et al. (2018). 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).

Behavioral observations

To characterize perch behavior of Barbary ground squirrels and test the predictions presented in Table 1, we used 10 min scan samples and all-occurrence sampling of perch bouts throughout each behavioral observation period in addition to performing 10 min focal follows (Altmann 1974). Table 1 also provides the behavioral observation method used to test our predictions.

In our scan- and all-occurrence sampling, 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. We defined a group 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 conducted behavioral

observations during all three field seasons between 10:00 h GMT and 2 h before sunset, i.e., when the squirrels are active above ground (Machado 1979; van der Marel et al. 2019). In 2014, we first established sites 1 and 2 at the beginning of the field season, while site 3 was set at the end, resulting in an unequal number of behavioral observations among sites this year (for a breakdown of the total observation periods, the number of scans, and hours observed per site and year see SM1). 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 provided an ethogram of all recorded behaviors in SM2). 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). Finally, we included the height from which the squirrels performed the behaviors. 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). Prim8 software measured the exact duration of perch behavior instead of the number of times the behavior was observed, which we used to analyse coordination of perch bouts by taking the proportion of time individuals were perched (predictions 2 and 3; Table 1). In our analyses, we selected individuals that were observed for at least 50 min over a minimum of five observation periods (Edwards and Waterman 2011).

To study perch behavior in more detail (predictions 1, 5, 6, 7, and 8, Table 1), we also performed 10 min focal follows in 2015 (Altmann 1974), recording focal follows for 81 individuals (ranging from 1 to 7 focal follows per individual). Before sampling, we recorded which of the three sites we sampled, focal ID, and the number and ID's of the individuals in sight

during an observation period (i.e. group size, see van der Marel et al. 2019). During the focal follow, we recorded the behavior (following the behaviors noted in the ethogram, SM2), location, the height of position (using a tape measure), the number of other individuals perching, and the distance from the focal to cover. We randomized the order of the site in which we performed focal follows using a random number generator (MS Excel 2013) and the order of focal follows among individuals observed in the site directly in the field using a randomizer application on an Android phone (Randomizer v. 0.2.6-beta, Mahé 2016). We only performed focal follows when no predators were observed, removing the possibility that individuals were responding to the same external stimulus (Beauchamp et al. 2012; McDougall and Ruckstuhl 2018).

Perch behavior general description

Using both the scan- and all-occurrence sampling to investigate whether all individuals perform perch behavior, we first calculated the percentage of individuals that perch from all marked individuals during the three field seasons. We then calculated the number of scans where one, two, or more than two individuals were perched, and the proportion of group members perched per scan excluding observations performed during the mating season. We analyzed the relationship between the proportion of perched group members and group size with a beta regression from the ‘betareg' package version 3.1-1 (Cribari-Neto and Zeileis 2010) and the likelihood ratio test from the ‘lmtest' version 0.9-36 (Zeileis 2002). To study whether perch behavior functioned as induced vigilance, we compared the proportion of perched individuals when a predator was observed or when we observed an alarm call (external stimulus present) *vs.* when no predator was observed or when no alarm call was heard (external stimulus absent) using

a Mann-Whitney *U* test due to the non-normality of the data (prediction 0; Table 1). To test whether individuals perch from elevated positions (prediction 1; Table 1), we used a Mann-Whitney *U* test to examine differences in height between perched squirrels and squirrels that performed any other behavior.

To measure coordination of perch bouts (predictions 2 and 3; Table 1), we calculated the difference between the observed and expected proportions of time when at least one individual was perched per group (Pays, Jarman, et al. 2007; Öst and Tierala 2011; Beauchamp 2015). 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 individual *i* is perched, i.e., total time spent perched divided by the total time observed for that individual (Beauchamp 2015; Bednekoff 2015). We used the number of observation periods as our sample size if the individuals seen in an observation period belonged to the same group. We measured the observed time as the sum of all perch bouts in the group divided by the sum that each individual in the group was observed. If the difference in proportions (p_{obs}-p_{exp}) did not differ from 0, then individual perch bouts were independent and not coordinated; 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). 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. We excluded days that females were in estrus because male behavior changed as they search competitively for estrous females, similar to what has been reported for the Cape ground squirrel (Waterman 1998). We excluded unidentified individuals because a different unidentified squirrel could have switched with the initial unidentified squirrel during a scan. Thus, start and endpoints of perch bouts could have corresponded to different unidentified squirrels. 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 observation period.

Perch behavior and social conditions analyses

To test whether adults and subadults spent more time perched than juveniles (prediction 4; Table 1), we calculated activity budgets for perch behavior, low-quality vigilance, and foraging of adults, subadults, and juveniles. We divided the number of scans in which each individual was observed performing each behavior by the total scans in which they were observed. In the absence of any sex differences in time allocation of low-quality vigilance and perch behavior (van der Marel et al. 2019), we tested for differences among adults, subadults, and juveniles for males and females combined. Since our data were not normally distributed, we used Kruskal-Wallis tests to account for differences in proportion time spent in low-quality vigilance, perch behavior and foraging for adults, subadults, and juveniles. If the results were significant, we performed post-hoc tests using a "Holm" correction (Holm 1979).

To examine whether individuals only perch when close kin are nearby (prediction 5; Table 1), we extracted information from our focal follows (N = 191) and analyzed relationships between individuals using genetics data extracted from van der Marel et al. (2020). Relatedness ranged from non-related (r = 0) to highly-related (r = 0.69), but the average within-group relatedness was 0.19 ± 0.01. We used generalized linear mixed models (GLMMs) to analyze the proportion of time spent perched in relation with multiple measures for both our independent variables (alone *vs.* in-group, kin-selection, and parental behavior), with ID as the random factor. We then compared the model against a null model using the likelihood ratio test from the ‘lmtest' version 0.9-36 (Zeileis 2002). We used a 'glmmADMB' with the beta distribution (Bolker et al.

2012; Fournier et al. 2012) on the proportion of time spent perched for kin (parent-offspring to first cousin; $r > 0.125$) *vs.* nonkin (unrelated to second cousin; $r < 0.125$), and a Spearman's rank correlation to test for a correlation between proportional time spent perched and relatedness of the group. To test whether perch behavior was a parental behavior (prediction 6; Table 1), we analyzed the time adult females spent perched in presence and absence of vulnerable offspring using a glmmADMB (Bolker et al. 2012; Fournier et al. 2012) with ID as a random factor.

Perch behavior and survival analyses

To study whether survival increased for perched individuals, we recorded whether perched individuals were closer to cover than individuals performing another behavior and whether individuals were perched when alone and, in a group (prediction 7; Table 1). We only used data from individuals that were both feeding and foraging within the 10 min focal follow. Since the average proportion of time spent perched was not normally distributed, we used a paired Wilcoxon signed-rank test to test for a difference in distance to cover for perched *vs.* feeding individuals. We then tested for differences in perch behavior when the individual was alone compared to when group members were present using a glmmADMB.

We considered individuals as survivors if the focal squirrels were trapped in the following field season (2016) to study whether survival decreased for perched individuals (prediction 8; Table 1). We measured survival as the last Julian day observed (number of days counted from our first fieldwork day, 12 February 2014 = Julian day 0) and age at disappearance. As we performed multiple focal follows on the same individual, we averaged the proportional time spent perched for analyses where we only had one measure per individual (survival, Julian date lived until, and age at disappearance). We tested whether perched individuals (proportional time

spent perched > 0.1) experienced higher predation risk than individuals that were not perched (proportional time spent perched < 0.1) using a Mann-Whitney *U* test. We performed a Spearman rank correlation on the proportion of time spent perched and the last Julian date observed and a Kruskal-Wallis test on age at disappearance. We calculated the proportion of time that each squirrel allocated to foraging and perch behavior, which we analyzed using a Spearman's rank correlation. 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) and tested the relationship between body condition and proportional time spent perched using a glmmADMB with ID as a random factor.

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 2009). We set statistical significance to the level of 0.05. Unless otherwise indicated, we denote averages as mean ± standard error (SE).

Results

Perch behavior general description

Overall, 99.3% of the squirrels (adults, subadults, and juveniles, $N = 139$) were observed perching. In 31.9% of a total of 3134 scans just one individual perched, while 2 or over 2 squirrels perched in 21.1 and 19.8% of scans, respectively. On average 38.4 ± 0.6 % of a group was perched per scan ($N = 522$ scans), but we found no relation between number of perched squirrels and group size (LR test: $\Lambda = 0.04$, $P = 0.85$). Individuals perched both in the presence and absence of predators (prediction 0 Table 1). Although, the percentage of individuals perched per scan when a predator was observed during the observation period (53.3 ± 1.3%, $N = 417$ scans) was significantly higher to that when no external stimulus was observed (48.9 ± 0.6%, *N*

= 2192 scans; Mann-Whitney *U* test: $U = 503630$, $P < 0.001$, effect size r = 0.07; prediction 0 Table 1). Barbary ground squirrels were located at more elevated positions when perched (N = 2203) compared to locations where the squirrels performed any other behavior (prediction 1 Table 1; $N = 5289$; Mann-Whitney *U* test: $U = 3958800$, $Z = -22.01$, $P < 0.001$, r = 0.25; Fig. 1). We found that the proportion of observed time that at least one individual in the group was perched (p_{obs}) was smaller than the proportion of expected time (p_{exp}, predictions 2 and 3; Table 2). Furthermore, p_{obs}-p_{exp} was smaller than 0 (prediction 2 and 3 Table 1, Table 2).

Perch behavior and social conditions analyses

We found differences in time spent foraging (Kruskal-Wallis test: $H_2 = 8.18$, $P = 0.02$, post-hoc adults-juveniles $P = 0.04$), low-quality vigilance (Kruskal-Wallis test: $H_2 = 6.64$, $P = 0.04$, post hoc subadults-juveniles $P = 0.03$) and perch behavior (Kruskal-Wallis test: $H_2 = 52.6$, $P < 0.001$, post-hoc adults-juveniles and subadults-juveniles $P < 0.001$) among age classes (prediction 4 Table 1, Fig. 2). Time spent perched did not differ when individuals performed perch behavior in the absence (33.5 ± 3.6%, $N = 77$ focal follows) or presence of kin (26.7 ± 2.4%, $N = 114$ focal follows; LR test: $\Lambda = 2.93$, $P = 0.09$; GLMM: 0.35 ± 0.20, random factor: ID = 0.25; prediction 5 Table 1). We found neither any correlation between perch behavior and relatedness (Spearman's rank correlation: $r_s = -0.05$, $P = 0.49$). Adult females ($N = 86$) spent a similar amount of time perched when vulnerable juveniles were absent (29.3 ± 3.3%, $N = 90$ focal follows) or present (30.7 ± 2.7%, $N = 80$ focal follows; LR test: $\Lambda = 0.39$, $P = 0.53$; GLMM: 0.12 ± 0.20, random factor: ID = 0.16; prediction 6 Table 1).

Perch behavior and survival analyses

In our 2016 field season, 50 of our focal animals from 2015 survived and 32 disappeared. We found that individuals were closer to cover when perched (0.58 ± 0.09 m) than when foraging (3.20 ± 0.32 m; paired Wilcoxon signed-rank test: $V = 41$, $N = 94$, $P < 0.001$; prediction 7 Table 1). Individuals that were alone or in groups spent similar amounts of time perched (37.3 ± 5.2%, $N = 38$, and 29.5 ± 2.0%, $N = 193$, respectively; LR test: $\Lambda = 0.61$, $P = 0.44$; GLMM: -0.19 ± 0.24, random factor: ID = 0.23; prediction 7 Table 1). We found no difference in survival, last Julian day observed, and age at disappearance with the proportion of time spent perched (N = 82 individuals, Mann-Whitney U test: $U = 803.5$, $P = 0.98$; Spearman's rank correlation: r_s= 0.04, $P = 0.73$; Kruskal-Wallis test: $H_5 = 1.46$, $P = 0.92$; respectively; prediction 8 Table 1). Foraging was negatively correlated to time spent perched (prediction 8 Table 1, Fig. 3), and perch behavior was not affected by body condition (LR test: $\Lambda = 0.24$, $P = 0.62$; GLMM: 0.54 ± 1.10, random factor: ID = 0.09).

Discussion

Barbary ground squirrels met two criteria of a sentinel system (van der Marel et al. 2019), but coordination of perch bouts was unknown. Here, we examined the importance of quantitatively testing coordination in species with a potential sentinel system. Barbary ground squirrels' perch behavior was coordinated; however, individuals did not take turns acting as sentinels as they never decreased the time between different perch bouts in a group. Instead, perch bouts were synchronized because the observed time without a perched individual was smaller than the expected time resulting in a difference in proportions smaller than zero (Table 2). We detected no relationship between the numbers of perched individuals and group size.

Furthermore, 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). Finally, we detected no apparent costs or benefits of perch behavior at the individual or group level. Thus, our result may impact the number of species with a true sentinel system because coordination of sentinel bouts has not been quantitatively tested for 37 out of 40 species with a described sentinel system (Bednekoff 2015). When taking turns in a potential sentinel system is tested, coordination may be absent altogether (Hing et al. 2019) or synchronized, as in our study.

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 perch behavior may be an individual's optimal activity, as is seen in suricates, *Suricata suricatta*, or Arabian babblers, *Argya squamiceps*, where individuals become sentinels when satiated (Clutton-Brock 1999; Wright, Maklakov, et al. 2001). We did not find a relationship between perch behavior and body condition, suggesting that Barbary ground squirrels on Fuerteventura may be able to afford a reduction in foraging behavior perhaps 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). Hence, satiated squirrels may perform perch behavior as an optimal activity and may imply that the trade-off between vigilance and feeding might be absent in the invasive population of Barbary ground squirrels.

A second mechanism to explain synchronized vigilance is the structure of the habitat because the presence of rock walls prevents the squirrels from looking on either side of the wall when on the ground. 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), which in turn can be considered a constraint on sociality. Hence, to adequately detect predators, two Barbary ground squirrels may be necessary to look in both directions of the rock wall. Therefore, perch behavior may simply be a form of extremely high-quality vigilance where individuals improve their level of detection by synchronizing vigilance bouts. 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, squirrels may be vigilant at the same time on top of rock walls to watch ‘each other's back’. As such, vigilance could mean that at least two or more individuals have to be on the lookout to watch at either side of the rock walls, instead of being a synchronized function as a form of collective sentinel behavior. The possibility of collective sentinel behavior requires further attention. Thus, the structure of the habitat (plains interspersed with ravines and rock walls), and that they are group-living, could influence the synchronization of vigilance in the invasive population of Barbary ground squirrels.

As we used an observational study in the field, overall vigilance levels, distance between neighbors, and group size could have affected levels of synchronization. For example, when vigilance levels are high in a group, there is a greater chance that multiple individuals are vigilant at the same time, whereas for groups where vigilance is overall low, there is less chance of detecting synchronization (Beauchamp 2015). Furthermore, monitoring of neighbors may prove too difficult when the distance between neighbors is too large (Pays et al. 2009), or when group sizes are too large (Beauchamp 2015), which may skew our results to synchronization instead of taking turns.

Although social conditions, including sex, kinship, age, or being a parent, may influence perch behavior, male and female Barbary ground squirrels spent the same amount of time perched (van der Marel et al. 2019). This lack of sex-biased benefit on perching suggests that perch behavior does not serve a function in intrasexual competition (Walker et al. 2016) or mate protection (Horrocks and Hunte 1986). Group members of species with a sentinel system are often closely-related (Fernández et al. 2003); however, the role of kin selection is not a prerequisite to the evolution of such a system (Bednekoff and Woolfenden 2003). We found that kin selection was not a mechanism explaining coordinated vigilance in Barbary ground squirrel – with varying relatedness levels within groups due to promiscuity– because individuals were perched independently of whether close kin was in their visible range or not. Adults and subadults performed more perch behavior than juveniles, but juveniles spent more time foraging than adults or subadults, which is similar to other bird and mammalian species (Rasa 1977; Ferguson 1987). In contrast to other species, e.g., common eiders, *Somateria mollissima* (Öst and Tierala 2011), we did not find that perch behavior increased for mothers when vulnerable young were present, refuting the notion that perch behavior in Barbary ground squirrels was a form of

parental care. In species where mothers show maternal care, such as ungulates, mothers provide extra vigilance so that their offspring can increase time spent feeding (Pays et al. 2012), which could explain our finding that juveniles do not spend perched a similar amount of time as adults. To summarise, environmental conditions may affect perch behavior in the Barbary ground squirrels on Fuerteventura more than social conditions.

Our results also suggest that perch behavior did not impose survival costs or benefits to the Barbary ground squirrel population on Fuerteventura because 1) distance to cover was shorter for perched individuals than foragers, and, 2) we found no relation between the proportion of time spent perched on survival. However, we were unable to measure predation risk directly for perched individuals compared to foragers and we may not have had enough variance in the time spent perched to detect an effect on survival. Individuals were as likely to perform perch behavior alone as in groups, suggesting a selfish benefit to the perched individual, such as increased detection of predators (Bednekoff 2001; Bednekoff and Woolfenden 2003). The absence of an effect on survival could be explained by two mechanisms: 1) all individuals that were observed in at least five scans in the population perform perch behavior, and, 2) there is an ecological release of predators and parasites in the invasive range of Barbary ground squirrels (López-Darias 2007; López-Darias and Nogales 2008; Piquet et al. 2018). In summary, we found no apparent cost or benefit of perch behavior in the invasive population of the Barbary ground squirrel.

Conclusions

Our results demonstrated the importance of testing for coordination in species with a suggested sentinel system and showed that the invasive population of Barbary ground squirrels

synchronize perch behavior. Two non-mutually exclusive hypotheses explaining synchronization of perch bouts are that: 1) squirrels are satiated and 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). Future studies could test for other possible hypotheses explaining synchrony of perch bouts, including contagion-of-fear, induced synchrony, and mimicking of nearest neighbor hypotheses (Sirot and Touzalin 2009; Beauchamp 2015). This study shows that quantitative testing of coordination is important in species with a described sentinel system and that the cost of the trade-off between vigilance and foraging may not be high for an invasive species.

Acknowledgements

We acknowledge the landowners of our study sites, the IPNA-CSIC by providing a research vehicle, and the Cabildo of Fuerteventura for the use of the facilities and the help of its staff at the Estación Biológica de La Oliva. AM was supported by a University of Manitoba Faculty of Science graduate studentship and a Faculty of Graduate Studies Graduate Enhancement of the Tri-Council Stipend (GETS). MLD was funded by the Program Agustín de Betancourt of the Cabildo Insular de Tenerife under the identification mark "Tenerife 2030" (P. INNOVA 2016-2021). JMW was funded by the National Research Council of Canada (#04362), the Canadian Foundation for Innovation, and the University of Manitoba University Research Grant Program. All methods in this study were approved by the University of Manitoba animal ethics committee (protocol #F14-032), were permitted by the government of Fuerteventura (Cabildo Insular de Fuerteventura #14885) and adhered to the ABS/ASAB guidelines for ethical animal research.

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Figure legends

Figure 1. Boxplot of height (m) of Barbary ground squirrels when perching or performing any other behavior. The dark line shows the median, the box edges the upper and lower quartiles, the whiskers are 50% from the median, and the closed circles are the outliers, calculated as the values smaller or larger than 1.5 times the box length (i.e., upper - lower quantile).

Figure 2. Mean ± SE of the proportion of time spent feeding, performing low-quality vigilance, or perching in adult, subadult and juvenile Barbary ground squirrels. Significant differences are denoted by asterisks (*P < 0.05; **P < 0.01; ***P < 0.001).

Figure 3. Relation between the proportion of time spent foraging and time spent perching (Spearman's rank correlation: $r_s = -0.38$, $P < 0.001$) in Barbary ground squirrels.

Tables and table legends

Table 1. Hypotheses and predictions on perch behavior (vigilance without performing any other behavior for over 30 s and at raised positions of at least 30 cm above the ground) in Barbary ground squirrels on Fuerteventura, Canary Islands, Spain.

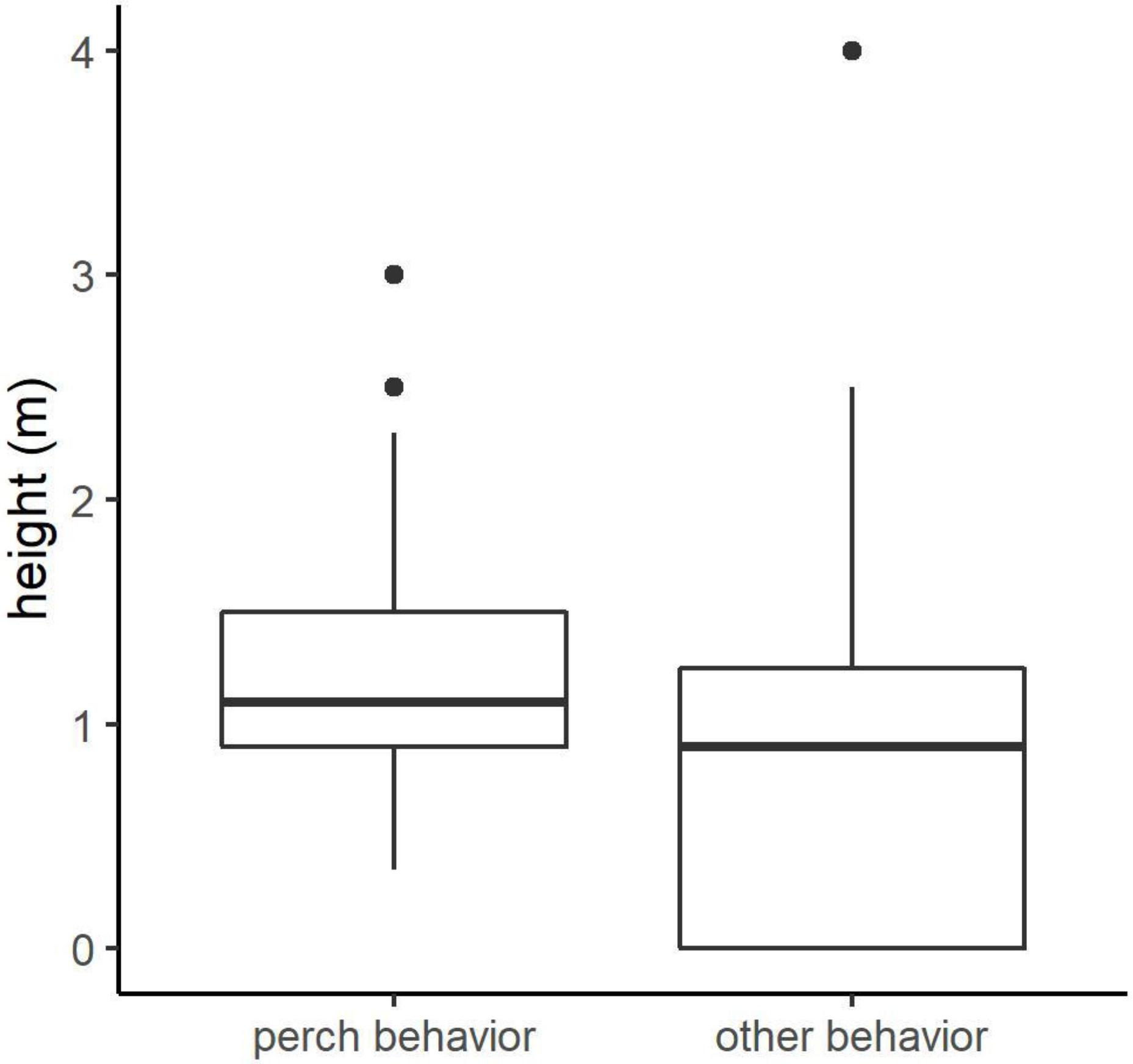
Hypothesis	Predictions	Method	Supported
Perch behavior			
Perch = induced vigilance	0) Individuals only perch in the presence of an external stimulus, e.g., predator	scan	no
Perch = sentinel behavior	1) perched from elevated positions	scan + ff	yes
	2) continuous turn-over without changing the number of perched individuals any more than expected by chance	all	no
Perch = synchronized behavior	3) either multiple individuals are perched or non-vigilant at the same time	all	yes
Perch behavior and social conditions			
Social conditions influence who are perched	4) adults and sub-adults spent more time perched than juveniles	scan	yes
	5) individuals only perch when close kin are nearby (kin-selected behavior)	ff	no
	6) adult females only perch when own vulnerable offspring have emerged (parental behavior)	ff	no
Perch behavior and survival			
Survival increases for perched individuals	7) perched individuals are closer to cover than individuals performing another behavior & individuals are perched when alone and in a group	ff	yes
Survival decreases for perched individuals	8) greater risk of predation when located at raised positions & when in worse body condition	scan + ff	no

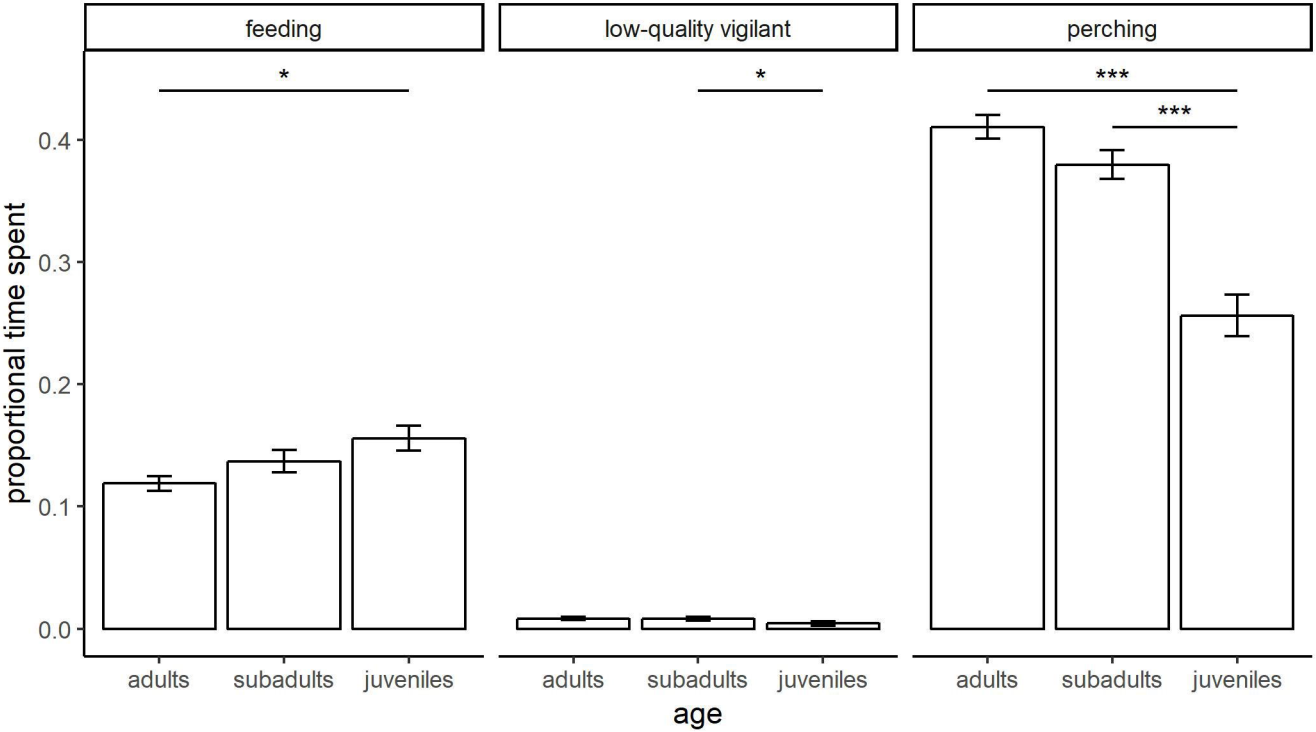
[a] Behavioral observation method used to test predictions: 10 min scan sampling (scan), all-occurrences during scan sampling (all), and separate 10 min focal follows (ff).

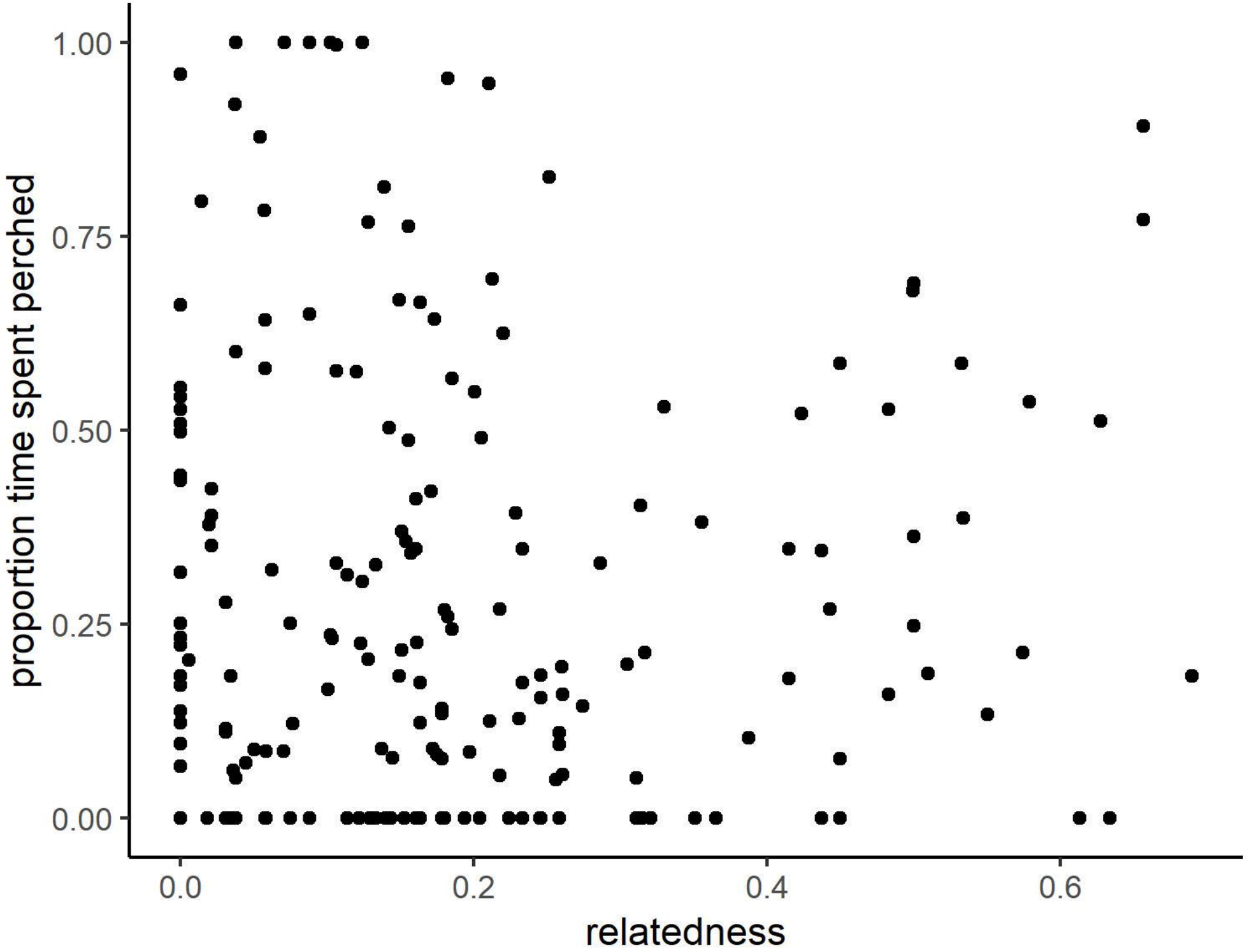
Table 2. The proportion of observed (p_{obs}) and expected (p_{exp}) time at least one individual was perched (mean ± SE) per observation period in Barbary ground squirrels calculated as duration of perch bouts.

Observation period	N	p_{obs}	p_{exp}	P_{obs}-P_{exp}	*V*	*P*
All individuals	125	0.19 ± 0.02	0.54 ± 0.03	-0.36 ± 0.03	496	<0.001
Adults	122	0.20 ± 0.02	0.52 ± 0.03	-0.33 ± 0.03	158	<0.001
Adult females	107	0.19 ± 0.02	0.52 ± 0.03	-0.35 ± 0.02	20	<0.001

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


height (m)
4
3
2
1
0
perch behavior
other behavior


feeding
low-quality vigilant
perching
*
*
***
***
0.4
0.3
0.2
0.1
0.0
proportional time spent
adults
subadults
juveniles
adults
subadults
juveniles
adults
subadults
juveniles
age


1.00
0.75
0.50
0.25
0.00
proportion time spent perched
0.0
0.2
0.4
0.6
relatedness