

Life history traits, social organisation and the drivers of sociality in an
invasive ground squirrel

by

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Thesis abstract

Sociality evolves when the benefits outweigh the costs of interacting with conspecifics and can be influenced by genetic, phylogenetic, life history, or ecological constraints. Many groups are formed by natal philopatry with the environment constraining levels of sociality. For example, diurnal rodents living in harsh environments can be social to avoid the costs of predation. I used the invasive population of the Barbary ground squirrel (*Atlantoxerus getulus*) on the arid island of Fuerteventura, Spain, as my study system to explore this idea. Two Barbary ground squirrels were introduced to Fuerteventura in 1965. As they are invasive, I first questioned whether **life history traits influenced their invasion success**. Then, I used observational, experimental and genetic data to investigate **whether they are social** and **whether predator avoidance is a selective pressure** influencing their social patterns by studying their vigilance and alarm vocalisations. Barbary ground squirrels have large and frequent litters, and thus show potential for rapid population growth with a generation time of approximately one year, which may have contributed to their invasion success. They are social, as both males and females interact throughout the day, but they show sexual segregation of sleeping burrows. As group size increased, individual vigilance did not decrease, but collective vigilance did increase and they use alarm calls to warn group members of danger. Hence, they show partial collective detection of predators. The absence of a group-size effect can be explained since the squirrels synchronise their vigilance bouts. Thus, the constraints of living as a diurnal species in an arid environment and predation pressure are possible selective pressures explaining sociality in the invasive Barbary ground squirrel. This thesis advances our understanding of sociality in African ground squirrels, but also provides valuable insight into population growth and corresponding invasion success of an introduced species, as invasive

species provide a unique framework to study evolution of sociality and population biology over a relatively short timeframe.

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Dedication

To my grandmother, Anneke Homan-van der Weel

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Chapter 1 General introduction

Sociality

Species can be placed on a spectrum of social systems. This spectrum ranges from species that do not share space with conspecifics, i.e., solitary species such as solitary bees (Danforth, Cardinal, Praz, Almeida, & Michez, 2013), to species that do share space but do not interact with conspecifics, called aggregations (Parrish, Hamner, & Prewitt, 1997), and species that share space and interact with conspecifics, i.e., social species. Social species may show high levels of sociality either by providing alloparental care and division of labour, e.g., eusocial insects and naked mole-rats (Danforth et al., 2013), or by having complex relationships with their group members in the form of dominance hierarchies or coalition formation (Lukas & Clutton-Brock, 2018), e.g., dolphins (Wiszniewski, Brown, & Möller, 2012). From these different patterns, sociality is defined as "any set of organisms, belonging to the same species that remain together for a period of time interacting with one another to a distinctly greater degree than with other conspecifics" (Wilson, 1975). Possible selective pressures leading to grouping may be genetic (Hamilton, 1964), phylogenetic (Sobrero, Inostroza-Michael, Hernández, & Ebensperger, 2014), ecological (Emlen, 1982), or sociobiological (Armitage, 1981; Blumstein & Armitage, 1998), and these pressures do not have to be exclusive (Thierry, 2008). Understanding the costs and benefits of sociality and the selective pressures responsible for the propensity of species to live in groups has been a major theme in behavioural ecology.

Constraints on sociality

Ecological constraints acting on group living are numerous. Group living can be favoured by living in a harsh environment (Lacey & Wiczorek, 2003), for example, through delayed

dispersal (Armitage, 1981; Barash, 1974), or by reduced thermoregulatory costs (Edelman & Koprowski, 2007; Hayes, 2000; Koprowski, 1996; Schradin, König, & Pillay, 2010). The availability and distribution of resources in terms of shelter, food and mates could also influence group living (Ebensperger, 2001). However, one of the main ecological constraints on group living is predator avoidance (Bertram, 1973; Hamilton, 1971; Pulliam, 1973).

Group living animals can avoid predation through multiple mechanisms. For example, an individual can use its group members as cover (the selfish herd hypothesis, Hamilton, 1971). On the other hand, individuals can also cooperate to deter a predator (i.e., group defence hypothesis, Owings & Coss, 1977; Waterman, 1997). Some species may live in groups because there is safety in numbers, meaning that the risk of predation is diluted by the number of individuals in the group, which is termed the dilution effect (Bertram, 1978). Or group living species increase the detection rate of predators, i.e., the collective detection or ‘many eyes’ hypothesis (Lima & Dill, 1990; Pulliam, 1973). Predictions for the last two hypotheses are quite similar, they both predict that individual vigilance decreases with increasing group size but only for the collective detection hypothesis collective vigilance increases with increasing group size (Bertram, 1978; Pulliam, 1973; Roberts, 1996). However, for the collective detection hypothesis to work, individuals have to use alarm communication to warn group members of danger (Fairbanks & Dobson, 2007).

Alarm communication requires a signaller and a receiver (Seyfarth & Cheney, 2003). Examples of cues that allow the detection of predators are chemical, olfactory, visual, and auditory cues (Bednekoff, 1997; Blumstein, 2007; Blumstein, Barrow, & Luterra, 2008; Clutton-Brock, 1999; Klump & Shalter, 1984; McNamara & Houston, 1992; Phillips & Waterman, 2013; Smith, 1992). Chemical signals are important alarm signals in aquatic species

(Bairos-Novak, Mitchell, Crane, Chivers, & Ferrari, 2017; Smith, 1992). The detection of predator odours is especially important in prey species that are nocturnal and/or mainly fossorial (Apfelbach, Blanchard, Blanchard, Hayes, & McGregor, 2005; Phillips & Waterman, 2013). Visual cues are essential for predator detection in diurnal species, whereby predator detection will be easier in a habitat with an open structure (Ylönen & Brown, 2007).

Investment in vigilance behaviour is considered to be a trade-off between feeding activity (energy gain) and time spent vigilant, which is dependent on the level of predation risk (Bednekoff & Lima, 1998). Individually, animals can increase their energy intake by performing low-quality vigilance (vigilance while performing another behaviour), while they enhance predator detection by performing high-quality vigilance, i.e., vigilance without performing another behaviour (Périquet et al., 2012; Unck, Waterman, Verburgt, & Bateman, 2009). Group living animals can coordinate vigilance to increase energy intake, either by taking turns acting as sentinels or by synchronising vigilance bouts (Beauchamp, 2015). Synchronisation of vigilance bouts occurs when group members are vigilant or non-vigilant at the same time (Beauchamp, 2015). Whereas vigilance is considered sentinel behaviour, when individuals forego feeding and take turns performing high-quality vigilance from raised positions with the assumptions that there is no change in number of individuals being on guard and that the individuals on guard warn group members of danger (Bednekoff, 1997; Bednekoff & Lima, 1998; Rasa, 1987). In terrestrial species, warning of group members is primarily achieved by visual or auditory signals, e.g., by tail flagging (McRae & Green, 2014) or alarm calling (Klump & Shalter, 1984), respectively.

Alarm vocalisations do not only have to function as a warning to group members, these alarm calls can also cause chaos, deter an attack by recruiting additional callers or by reducing

the predator's patch quality, or convey information on a predator's location or type, the level of risk and the urgency to respond (Blumstein, 2007; Klump & Shalter, 1984; Macedonia & Evans, 1993; Manser, 2001). Since animals are constrained by their vocal tract (Fitch, 2000), they may use different mechanisms to extend their vocal repertoire and to increase the information content of the calls (Arnold & Zuberbühler, 2008; Collier, Townsend, & Manser, 2017; Jansen, Cant, & Manser, 2012). For instance, individuals could change the order of the elements within a syllable; add an element to a syllable; and vary the call type, the duration of call bout, the rate and amplitude of calls, and the number of callers (Blumstein, 2007; Blumstein, Verneyre, & Daniel, 2004; Engesser, Ridley, & Townsend, 2016; Ouattara, Lemasson, & Zuberbühler, 2009; Sloan & Hare, 2004, 2008; Warkentin, Keeley, & Hare, 2001). The alarm call receiver(s) can then use the information conveyed in the call to assess environmental risk and to make appropriate decisions to avoid predation.

Rodents as a study system

Rodents offer an excellent study system to define the selective pressures that influence sociality because 1) the species are found along a continuum of the sociality spectrum (Wolff & Sherman, 2007), and 2), are widely distributed resulting in differences in environmental conditions they live in. Rodents, thus, provide the potential for studies on related species with different selective pressures influencing social evolution. For example, diurnal semifossorial species living in arid environments are often social to avoid predation (Randall, 2007); whereas, in semifossorial temperate ground-dwelling squirrels (tribe Marmotini) predation risk, a short growing season, and body size influences sociality levels (Armitage, 1981; Barash, 1974; Blumstein & Armitage, 1998; Matějů et al., 2016; Michener, 1983). The African ground squirrels

(tribe Xerini) – a sister tribe to the tribe Marmotini – do not have the ecological constraint of a short growing season, but instead, experience different selection pressures, e.g., low and unpredictable amount of rainfall (Shenbrot, 2014), which may influence their social organisation (Schradin et al., 2012). Yet, only one of the six species in this taxa have been studied extensively and little information is available for the other species.

Objectives and thesis organisation

The objective of my thesis is to examine whether ecological constraints created by an arid environment and predator avoidance are the selective pressures that define sociality in the small-bodied Barbary ground squirrel, *Atlantoxerus getulus*, the only species of the genus *Atlantoxerus* (Kryštufek, Mahmoudi, Tesakov, Matějů, & Hutterer, 2016). The small amount of information published on the social system of the Barbary ground squirrel is contradictory; Machado (1979) suggests that they are gregarious, whereas Gouat & Yahyaoui (2001) suggests that the males are either solitary or live together with the females in small family groups depending on the reproductive stage.

Barbary ground squirrels are endemic to Morocco, where they live in rocky and arid environments, but were introduced to the island of Fuerteventura, Spain, in 1965 (Machado, 1979). Since their introduction the population has spread across the island and their population is estimated at a million animals (López-Darias, 2007). Therefore, this island population is considered invasive because it is widespread and abundant (Colautti & MacIsaac, 2004). Despite its invasive character, it is still reasonable to study this population as habitats in Morocco are very similar to those in Fuerteventura and previous relevant studies on the species are only available on the invasive island population (López-Darias, 2007). Additionally, invasive

populations are hypothesised to be released of enemies (Colautti, Ricciardi, Grigorovich, & MacIsaac, 2004; Keane, 2002). The invasive population has reduced parasite diversity and abundances compared to the endemic population (López-Darias, Ribas, & Feliú, 2008), and predation pressure may be low in this population, suggesting the invasive Barbary ground squirrels will have low levels of sociality. As the invasive population was founded with only two individuals, the number of founders or the number of times introduced, also called the introduction effort (Blackburn, Lockwood, & Cassey, 2015; Colautti, Grigorovich, & MacIsaac, 2006; Lockwood, Cassey, & Blackburn, 2005; Simberloff, 2009), is not the main factor that contributed to their invasion success. Other factors that affect invasion success include habitat (Kolar & Lodge, 2001; Lodge, 1993) and species characteristics (Capellini, Baker, Allen, Street, & Venditti, 2015; Fisher & Owens, 2004; Hayes & Barry, 2008; Kolar & Lodge, 2001; Lodge, 1993). Especially, fast life history traits, such as early maturity and frequent and large litters, influence the success of introduced mammals because these traits promote population growth (Capellini et al., 2015), which is essential for a founding population to become invasive.

I wrote this thesis in manuscript form and it contains five data chapters addressing life history, social organisation, and the selective pressures influencing sociality in the Barbary ground squirrel. First, I studied life history traits of Barbary ground squirrels and examined whether a fast life history strategy is related to invasion success in mammals and specifically squirrels (Chapter 2). Next, I investigated whether ecological constraints are a predictor of sociality in African ground squirrels by examining the social organisation of the Barbary ground squirrel (Chapter 3). I examined whether predation risk affects grouping by studying the collective detection and dilution effect hypotheses in Chapter 4 and alarm communication in Chapter 5. In my final data chapter, I investigated whether high-quality vigilance in Barbary

ground squirrels is coordinated (Chapter 6). Collectively, these chapters address the knowledge gap that exists in the sociality literature on the selective pressures that influence grouping in African ground squirrels, which will aid in our understanding of the evolution of sociality in general.

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Chapter 2 Exploring the role of life history traits and introduction effort in understanding invasion success in mammals

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AM led the formulation of the research questions, hypotheses and study design, collected the data, performed the analyses, interpreted the data, and wrote the manuscript. MLD and JMW contributed to the study design, assisted with data collection, provided feedback on the written manuscript, contributed to critical revision of the work, and supported this research both logistically and materially.

Abstract

Invasive species – species that have successfully overcome the barriers of transport, introduction, establishment, and spread – are a risk to biodiversity and ecosystem function. Factors influencing invasion success include introduction effort (number of founders and introductions events), habitat, and species characteristics. Although introduction effort is still one of the main factors attributed to invasion success, life history traits are also important as they influence population growth. Successful invasive mammal species share life history traits (a fast life history) that select for more fecund species at the introduction, establishment, and spread stage. We examined what life history traits contributed to the invasion success of species where introduction effort is extremely low. We used the invasive Barbary ground squirrel, *Atlantoxerus getulus*, on the island of Fuerteventura, Spain, as our study system, because only a single introduction of two individuals from one source location has been reported. We also investigated the contribution of life history traits on the invasion success of mammalian and specifically squirrel species with a low vs a high introduction effort. We found that Barbary ground squirrels were on the fast end of the “fast-slow continuum” of life history, which may have contributed to their invasion success. However, none of the studied life history traits differed between invasive mammalian species with either a low vs a high number of introduction events, whereas for squirrel species a longer reproductive lifespan instead of high reproductive output or number of founders influenced whether they successfully spread in their introduced range. This study shows that invasion success cannot be predicted by just one characteristic and increases our understanding of the factors influencing invasion success in mammalian species.

Keywords: Barbary ground squirrel, fast-slow continuum, introduction effort, invasive species, life history, population dynamics

Introduction

Introduced species are a threat to biodiversity and ecosystem function, are an economic concern, and cause multiple conservation problems (Allendorf & Lundquist, 2003; Kolar & Lodge, 2001; Lodge, 1993; Tsutsui, Suarez, Holway, & Case, 2000). Introduced species become invasive when they successfully overcome barriers related to the four different stages of the invasion process (i.e., transport, introduction, establishment, and spread; Blackburn et al., 2011; Colautti & MacIsaac, 2004). Factors contributing to invasion success, which are mainly introduction effort (number of founders and/or introduction events), habitat, and species characteristics, can differentially impact the probability for a species to successfully overcome each stage (Blackburn et al., 2011). A greater number of founders promotes invasion success as they reduce extinction probability and enable populations to more readily adapt to new environments (Blackburn, Lockwood, & Cassey, 2015), and multiple introductions increase the probability for genomic admixture and increased fitness (Keller & Taylor, 2010). Habitat characteristics influence invasion success (Kolar & Lodge, 2001; Lodge, 1993) as they affect the adaptive potential of the introduced species (Le Roux, Wicczorek, & Meyer, 2008; Vahsen, Shea, Hovis, Teller, & Hufbauer, 2018). Finally, species characteristics promoting expansion success are related to certain life history traits: explorative and dispersive behaviour, a generalist character of the species and genetic variation among the introduced individuals (Capellini, Baker, Allen, Street, & Venditti, 2015; Fisher & Owens, 2004; Hayes & Barry, 2008; Kolar & Lodge, 2001; Lodge, 1993). In particular, life history traits promoting population growth are important at two different stages: 1) the introduction stage, because particularly at first, stochastic events can lead to higher risk of extinction, suggesting that smaller founding populations with slow population growth may be more susceptible to extinction risk (Capellini et

al., 2015); and, 2) the spread stage, because life history traits influence population growth, which is essential when dispersing individuals form new populations in their introduced range (Capellini et al., 2015).

Life history strategies of species can be placed along a “fast-slow continuum” (Bielby et al., 2007; Dobson & Oli, 2007; Promislow & Harvey, 1990; Stearns, 1983). Fast species – species with life history traits that accompany rapid population growth, such as early maturity and frequent and large litters – are generally short-lived with greater fecundity, while species on the slow end of the continuum are long-lived with lower fecundity (Dobson & Oli, 2007b; Promislow & Harvey, 1990; Stearns, 1983). Nonetheless, species within orders or even populations within species can show variation along this continuum (Dobson & Oli, 2007b, 2007a). Bat species, for example, may show a combination of life history traits either related to a fast or slow life history (Culina, Linton, Pradel, Bouwhuis, & Macdonald, 2019). In invasion ecology, fast life history traits are suggested to promote population growth and spread of introduced species, thus favouring species ‘invasiveness’ (Capellini et al., 2015). Mammals are more likely to be introduced if they have larger, more frequent litters and a longer reproductive lifespan (Capellini et al., 2015). The establishment success of introduced mammals depend on larger litters, longer reproductive lifespan and greater introduction effort, and their spread success is associated with larger, more frequent litters and higher introduction effort (Capellini et al., 2015). A fast life history influences not only invasion success in mammals (Capellini et al., 2015, but see Sol, Bacher, Reader, & Lefebvre, 2008), but also in reptiles, amphibians (Allen, Street, & Capellini, 2017; van Wilgen & Richardson, 2012), and fishes (Liu, Comte, & Olden, 2017). In birds, on the contrary, a slow life history increases the potential to be a successful

invader (Sæther et al., 2004; Sol et al., 2012). Thus, for different species, diverse life history traits may influence their potential for invasion success.

Nevertheless, introduction effort is considered to be the major factor amongst those affecting invasion success (Blackburn et al., 2015; Colautti, Grigorovich, & MacIsaac, 2006; Lockwood, Cassey, & Blackburn, 2005; Simberloff, 2009). Thus, both fast life history traits and a high introduction effort contribute to the probability for established species to successfully spread in the new range (Allen et al., 2017; Capellini et al., 2015). However, the role of introduction effort in explaining species invasiveness could be difficult to interpret in certain taxonomic groups, such as squirrels, as some species are known to be successful invaders without a high introduction effort. For example, in 71.4% of successful invasions of grey squirrels, *Sciurus carolinensis*, the number of founders did not explain invasion success, as fewer than ten individuals were released (Lawton, Cowan, Bertolino, Lurz, & Peters, 2010; Wood, Koprowski, & Lurz, 2007). Also in the Pallas's squirrel, *Callosciurus erythraeus*, and the Finlayson's squirrel, *Callosciurus finlaysonii*, the number of founders did not prevent them from establishing in their introduced ranges, as fewer than seven individuals were released (Benitez, Almada Chavez, Gozzi, Messetta, & Guichón, 2013; Bertolino, 2009; Bertolino & Lurz, 2013).

We used the Barbary ground squirrel as an exemplar of a species whose introduction effort is extremely low, as only two individuals from Morocco were introduced in 1965 to the island of Fuerteventura, Canary Islands, Spain (Machado, 1979). In 37 years, the Barbary ground squirrel had spread across the entire island, favoured by five translocation accounts from the original founder locality to new localities on the island (Machado, 1979; Machado & Domínguez, 1982; López-Darias, unpubl. data). Since the introduction, their population has grown to an estimated one million animals (López-Darias, 2007). The species has negative

ecological, economical, and public health impacts. They consume native and endemic snails (Groh & García, 2004; López-Darias, 2007; Machado & Domínguez, 1982), prey upon some critically endangered species (Bañares, Blanca, Güemes, Moreno, & Ortiz, 2003) and feed upon the eggs of small native and endemic passerine birds (López-Darias, 2007). Their ecological impacts go beyond direct predation upon species, as they directly alter plant-animal interactions of fleshy-fruited plant species and ruderal weeds, including herbaceous plants of native or introduced origin (López-Darias & Nogales, 2008; López-Darias & Nogales, 2016). Although reliable studies are lacking, it is thought to compete with the endemic shrew, *Crocidura canariensis* (López-Darias, 2008), listed as vulnerable by the IUCN (Hutterer, 2008). Moreover, these ground squirrels also alter the population dynamics of predators (López-Darias, 2007); first because they are the main prey of an endemic subspecies of Eurasian buzzard, *Buteo buteo insularum*, whose population has increased on Fuerteventura in the last 40 years possibly because they prey upon this abundant, new prey (Gangoso, Donázar, Scholz, Palacios, & Hiraldo, 2006; López-Darias, 2007), and second, as they are positively impacting invasive feral cat populations (Medina, López-Darias, Nogales, & García, 2008). Lastly, these ground squirrels are known to carry parasites that impact native fauna as well as public health (López-Darias, Ribas, & Feliú, 2008; Lorenzo-Morales, López-Darias, Martínez-Carretero, & Valladares, 2007), and to cause damage to agricultural activities (López-Darias, 2007; Machado & Domínguez, 1982). Despite the notable invasion success of the species on the island, nothing is known about the life history traits that could have influenced their population growth, and which, in addition to contributing to our understanding of invasion success when introduction efforts are minimal, are essential to plan for future conservation programs on this species.

The objective of this chapter is two-fold. First, we investigated life history traits of the Barbary ground squirrel, *Atlantoxerus getulus*, a species with a remarkably low introduction effort (Machado, 1979), and compared these traits to other successfully invaded mammals and squirrels. Second, we compared life history traits of mammalian species with high and low introduction efforts measured as the number of introduction events using the dataset provided by Capellini et al. (2015), and investigated whether number of founders and/or a fast life history influences invasion success of squirrels using the dataset provided by Bertolino (2009). This study, therefore, contributes to our understanding of the role of introduction effort and life history traits in explaining invasion success both in mammals and squirrels.

Methods

Life history traits of the invasive Barbary ground squirrel

Of the Canary Islands' seven main volcanic islands, Fuerteventura is the closest to the African continent (approximately 100 km away), the oldest, and has the second lowest altitude (807 m a.s.l.). The island has an arid climate – high temperatures (≈ 20 °C) and low rainfall (on average < 100 mm/year) – characterised by trade winds, which have resulted in a semi-desert habitat (López-Darias & Lobo, 2008). We studied the invasive population of Barbary ground squirrels in the area of Tindaya in the northwest of Fuerteventura (28°34'60" N, 13°58'0" W), which is characterised by stony plains with xerophytic scrubland, interspersed with ravines caused by erosion and abandoned cultivated areas that are fenced by man-made rock walls and dams. These rock structures function as shelter and lookouts for the ground squirrels (López-Darias & Lobo, 2008; van der Marel, López-Darias, & Waterman, 2019).

To determine life history traits of the species, we trapped Barbary ground squirrels using live traps (Tomahawk Co., WI, U.S.A.; 13 x 13 x 40 cm) baited with peanut butter (McEnnedy peanut butter, LIDL LLC, U.S.A.) during three consecutive years (February through July 2014, January through July 2015, and January through June 2016). We covered traps with cardboard to minimise heat-induced stress and we checked the traps every 40 to 60 minutes to reduce confinement stress. Upon capture, squirrels were transferred to a conical handling bag (Koprowski, 2002), where every adult squirrel received a sterile 0.1 g, 2.1 X 12 mm passive integrated transponder (PIT) tag (Avid Identification Systems, Inc., Norco, CA, U.S.A.) for individual identification.

We first assessed whether there was a distinct breeding season in the Barbary ground squirrels by regularly trapping and observing male (2014: $n = 32$, 2015: $n = 52$, 2016: $n = 55$) and female (2014: $n = 40$, 2015: $n = 69$, 2016: $n = 82$) reproductive progress. We reported the reproductive status of adult males through the year from non-scrotal to descending scrotum, fully scrotal, and regressing scrotum. Subadult males (2014: $n = 8$, 2016: $n = 1$) were those individuals that have reached adult body size, were over six months old, but did not have descended testes (Waterman, 1996). Female subadults (2014: $n = 6$) were individuals that have reached adult body size, were over six months of age, but their vulva and nipples were not swollen during the mating season (indicative of no reproduction). We assessed the reproductive progress of adult females by measuring gestation length from oestrus date until parturition date. We estimated the day of oestrus following previous recommendations by Pettitt, Waterman, & Wheaton (2008) and Waterman (1996). Lactation length was measured from the day of parturition to the day of juvenile emergence. Day of parturition was determined by trapping and weighing the females more extensively around their expected parturition date and by palpating their lower abdomen

for embryos. The nipples of immature (subadult) females are small but after their first successful parturition, the nipples elongate and swell during lactation, while large bite marks surrounding the nipples indicated the weaning period. We calculated the weaning age from the day of juvenile emergence until the bite marks around the nipples of the mothers started to subside. After weaning, the nipples of adult females stay elongated but not swollen (Waterman, 1996). We estimated age at first birth in females with known date of birth ($n = 8$). As our sample size was small, we also estimated age at first birth in females with unknown day of birth but instead with known date of emergence. For these females, we added the average lactation length to the date of emergence to acquire their age at first birth. We only used females, because we were certain they had mated due to the swelling of their vulva and presence of copulatory plugs. As age at first birth violated the assumptions of the normality and homoscedasticity of a parametric test, we tested for a difference in our two estimates (females with known date of birth vs females with known date of juvenile emergence) using a Mann-Whitney U test.

To locate nest burrows of adult pregnant females, we fitted them with radio collars (3.6 g PD-2C transmitters, Holohil Systems Ltd., Carp, Ontario, Canada) just prior to juvenile emergence. We radiotracked the females using an R-1000 telemetry receiver (Communications Specialists, Inc., Orange, CA, U.S.A.) and a Yagi antenna model F150-3FB (Advanced Telemetry Systems, Inc., Isanti, MN, U.S.A.). Upon juvenile emergence, we extensively trapped at nest burrows to sex, measure, and mark the juveniles (individuals newly emerged from their nest burrow up to six months of age) with ear tags (#1005 Size 1 Monel, National Band and Tag Co., Newport, KY, U.S.A.). We also determined litters per year and litter size. We used a Kruskal-Wallis test to analyse differences in average litter size across years. We calculated litter sex ratio as the proportion of male juveniles out of the total emerged juveniles (Charnov, 1982;

Ryan, Anderson, Gardiner, & Hare, 2012), which we analysed using a chi-square test of independence. We tested whether litter sex ratio differed from parity using an exact binomial test. Using a chi-square test of independence, we analysed differences in juvenile survival rate measured as the proportion of emerged juveniles that survived to one month. Occasionally, mothers merged their litters with the litters of other adult females before all juveniles were trapped and marked, resulting in unmarked juveniles at a communal burrow. These litters were excluded because we were uncertain of the identity of the mothers. Finally, we calculated maternal success rate as the proportion of females successfully raising their litter to emergence and used a chi-square test of independence to test for differences in maternal success rate.

We were unable to measure neonatal body mass in the field because the females give birth within their nest burrow, therefore we used neonatal body mass recorded during an earlier study on the Barbary ground squirrels on Fuerteventura (mean \pm SE = 8.1 \pm 0.5 g, n = 5 juveniles; Machado & Domínguez, 1982). We measured adult body mass using a spring scale (\pm 5 g; Pesola AG, Baar, Switzerland) and focused on masses outside of the reproductive period, selecting males that were non-scrotal and females prior to the breeding season or after their offspring were weaned. We measured average adult lifespan for individuals with known age and for individuals of uncertain age, thus, individuals that did not survive into adulthood were excluded. We tested for sex differences in average lifespan using Mann-Whitney U tests. We calculated adult survival as the proportion of adults in a group that were trapped in the following field season (January 2015, 2016, and 2017). We censored adult survival for squirrels that were already adults in our first field season and were still alive in our last field season, i.e., squirrels with uncertain age. We performed the Kaplan-Meier approach on our censored data using the ‘Survival’ package version 2.43-1 (Therneau, 2015; Therneau & Grambsch, 2000). Reproductive

lifespan was calculated from the maximum lifespan/longevity (5.0 year) reported in Aulagnier, Gouat, & Thévenot (2013) transformed into days and age at first birth in days following Capellini et al. (2015).

Finally, to explore differences between certain life history traits (gestation length, weaning age, age at first birth, litters per year, litter size, neonatal body mass, adult body mass, and reproductive lifespan) of mammalian species (excluding squirrels) and squirrel species (including the Barbary ground squirrel) that successfully invaded their new range (Appendix Table A1, Capellini et al., 2015), we used Mann-Whitney *U* tests, since all the selected life history traits violated the assumptions of parametric tests.

All procedures conformed to the guidelines of the American Society of Mammalogists for the use of wild mammals in research, were approved by the University of Manitoba Animal Care and Use Committee (protocol #F14-032), and were permitted by the government of Fuerteventura (Cabildo Insular de Fuerteventura #14885).

Life history vs introduction effort in explaining invasion success of mammals and squirrels

We first compared life history traits (gestation length, weaning age, age at first birth, litters per year, litter size, neonatal body mass, adult body mass, and reproductive lifespan) of mammals that successfully invaded their current habitat with a high vs a low introduction effort, defined as the number of locations the species was introduced to, which was transformed to a binary variable (following Capellini et al., 2015). We used quartiles to discriminate between species with a low and a high introduction effort, therefore we divided the species into two groups: species with a low (introduction effort < lower quartile) and a high (introduction effort > upper quartile) number of introduction events. We then tested for a difference in life history traits

of successfully invaded mammal species with a high or low introduction effort using Mann-Whitney U tests and we used the “Holm” correction to control for the false discovery rate in conducting multiple univariate tests (Holm, 1979).

Second, we used a generalised linear mixed model (GLMM) to test the impact of life history traits and number of founders on the invasion status of squirrels (successfully spread vs not-successfully spread) as we had multiple introduction events per species ($n = 8$ species ranging between 1 and 28 introduction events with 88 data points in total, Appendix Table A2, Bertolino, 2009). We used a GLMM for binomial distribution using the ‘lme4’ package version 1.1-18-1 (Bates, Mächler, Bolker, & Walker, 2015). To reduce the number of life history traits we only selected the traits that were shared by invasive mammals, i.e., litter size, litters per year, reproductive lifespan, and introduction effort (Capellini et al., 2015). We then tested for collinearity between our variables using the variance inflation factor (VIF) function from the ‘CAR’ package version 3.0-2 (Fox & Weisberg, 2011). None of our covariates had a VIF higher than three, therefore we included all independent variables (Zuur, Ieno, & Elphick, 2010). We included species as a random factor. We performed model selection using Akaike’s information criterion (AIC_c) (Harrison et al., 2018) in the ‘MuMIn’ package version 1.42.1 (Barton, 2018). We considered models with a difference between a model’s AIC_c and minimum AIC_c (ΔAIC_c) of two or smaller competitive (Burnham & Anderson, 2002), but then we considered the most parsimonious model the best (Arnold, 2010). From the best-supported model, we presented the predictor estimates, the 85% confidence intervals, and the odds ratios of the fixed factor(s) and the variance for our random factor (Arnold, 2010; Bolker et al., 2009). We calculated the goodness-of-fit of the model including only the fixed effects, called the marginal R^2 (R^2_m), and the conditional R^2 (R^2_c), which explains the variance of the model including both fixed and

random effects (Nakagawa & Schielzeth, 2013, 2016) using the ‘piecewiseSEM’ package version 2.0.2 (Lefcheck, 2016). We performed all the statistical analyses with alpha set to 0.05 in R version 3.5.1 (R Core Team, 2017). We reported the mean \pm standard error (*SE*).

Results

Life history traits of the invasive Barbary ground squirrel

Reproduction in the Barbary ground squirrels was seasonal; in 2014, mating started at the end of January and ended mid-March, whereas in 2015 and 2016 mating started at the beginning of January and late December and ended mid-February and at the end of January, respectively. Males were scrotal for 76.3 ± 4.0 days ($n = 65$) after the last day of the mating period, but it took on average 152.1 ± 5.0 days ($n = 54$) for males to fully regress their scrota. All adult females that we sampled within a group bred. Gestation length was 43.5 ± 0.4 days (range 39-49 days; $n = 47$ females) and lactation lasted 42.3 ± 0.5 days (range 39-46 days; $n = 43$ females). For the majority of females, age at first birth was the first breeding season. The estimates of age at first birth calculated for females with known date of birth (343.4 ± 11.0 days, $n = 8$) and for females with known date of emergence (345.5 ± 5.7 days, $n = 15$) did not differ (Mann-Whitney *U* test: $U = 53$, $P = 0.67$). Therefore, average age of first birth was 344.8 ± 5.2 days ($n = 23$ females).

Over a two-year period (2015 and 2016), 15 of a total of 138 pregnancies failed (10.9%). Females rebred in 11 of these failed pregnancies (73.3%), although five of these later pregnancies failed again (45.5%). Maternal success rate (proportion of females that successfully raised their litter to emergence) did not differ among years (2014: 0.78, 2015: 0.76, and 2016: 0.79; chi-square test of independence: $\chi^2_2 = 0.71$, $P = 0.70$). In 2016, eight females of a total of 80 (10.0%) were observed to have a second litter in one breeding season after they had

successfully bred once, but we do not have data on their litters because we left the field before the emergence of these late litters. In 2014, 112 juveniles emerged from 28 litters; in 2015, 161 juveniles from 44 litters; and in 2016, 166 juveniles from 63 litters. Average litter size did not differ among years (2014: 2.3 ± 0.3 , 2015: 3.4 ± 0.4 , and 2016: 3.1 ± 0.2 ; Kruskal-Wallis test: $H_2 = 3.91$, $P = 0.14$). The mean percentage of adult females that were successful in raising one litter during the three-year period was $75.5 \pm 2.0\%$, with a litter size of 3.0 ± 0.2 [1 – 8] juveniles/litter ($n = 62$ litters). Litter sex ratio was 0.50 male across all years and did not differ among years (2014: 0.50, 2015: 0.47, and 2016: 0.52; chi-square test of independence: $\chi^2_2 = 0.24$, $P = 0.89$), nor did it differ from parity (exact binomial test: two-tailed $P = 1.0$, 95%-CI = [0.42 - 0.59], $n = 45$ litters from 40 distinct females). Juvenile mortality was significantly lower in 2014 (19.4%) compared to 2015 (50.3%) and 2016 (49.4%), respectively ($\chi^2_2 = 31.24$, $P < 0.001$).

Average adult body mass outside of the reproductive season was 221.1 ± 5.7 g ($n = 116$ individuals) with males weighing 227.0 ± 6.4 g, $n = 51$, and females weighing 204.0 ± 5.0 g ($n = 65$). As average lifespan did not differ between adult males and females (lifespan of individuals of known age, Mann-Whitney U test: $U = 247.5$, $P = 0.20$; and lifespan of individuals of uncertain age included, $U = 10187$, $P = 0.95$), we combined the sexes. The estimated average lifespan of the Barbary ground squirrel in our sites calculated over a three-year span was 1.48 ± 0.09 years of age for the individuals with known age ($n = 52$), but 1.76 ± 0.06 years when individuals with uncertain age were included ($n = 239$). The survival rate did not differ between males and females ($P = 0.41$) and was 0.89 ± 0.02 , 0.79 ± 0.03 , and 0.73 ± 0.04 at age 1, 2, and 3 years, respectively. Reproductive lifespan calculated using the maximum lifespan/longevity of five years (Aulagnier et al., 2013) was 1480.2 days (4.1 years).

The Barbary ground squirrel is small-bodied compared to other invasive mammals, even compared to other invasive squirrels (Table 2.1). Invasive squirrels (squirrels that successfully spread in their new range) weighed less than other invasive mammals, but none of the other traits differed (Table 2.1).

Life history vs introduction effort in explaining invasion success of mammals and squirrels

Species with 9 or fewer introduction events (lower quartile) were considered to have a low introduction effort, while species with an introduction effort greater than 50 introduction events (upper quartile) were considered to have a high introduction effort. None of the life history traits differed between mammalian species that successfully spread with either a high or a low introduction effort (Table 2.2), neither did the “Holm” correction result in any significant differences (Holm, 1979).

The model with life history traits best explained whether squirrels were successful invaders or not irrespective of the number of founders (Table 2.3). Squirrel species that were successful invaders had a longer reproductive lifespan (Table 2.4, Fig. 2.1). The addition of species as a random effect (R^2_c) did not increase the variance explained by the predictors in the models, i.e., the variance explained was similar for the model with our fixed effects (R^2_m) alone compared to the model including the random effect (R^2_c) (Table 2.3).

Discussion

Our study provides the first detailed data on the life history and population dynamics of an invasive population of Barbary ground squirrels, a species with one of the lowest introduction efforts (one pair of individuals as founders) but great invasion success compared to other

introduced mammals (Capellini et al., 2015). The Barbary ground squirrel represents the fast end of the “fast-slow continuum” of life history traits, because they are small-bodied, mature within their first year and females have large and frequent litters. Additionally, we found that none of the life history traits differed between mammalian species with a low or a high number of introduction events and we demonstrated that life history traits, particularly reproductive lifespan, but not the number of founders, are related to invasion success in squirrels.

Life history traits of the invasive Barbary ground squirrel

Besides a fast life history, other aspects may have favoured the invasion success of the Barbary ground squirrel. First, although a small founding population suggests limited genetic diversity, which is considered detrimental (Dlugosch & Parker, 2008, but see Tsutsui et al., 2000), it is possible that the population preserved much of the genetic variation of the founders by reproducing rapidly after their introduction (Nei, Maruyama, & Chakraborty, 1975). On the contrary, a high degree of inbreeding may also lead to inbreeding depression, i.e., a high impact of deleterious alleles on the average fitness of offspring (Ralls & Ballou, 1982; Ralls, Brugger, & Ballou, 1979). But, the particular case of the Barbary ground squirrel, with a population estimated at around one million individuals (López-Darias, 2007), argues against inbreeding depression, because this population has successfully reproduced and grown.

Second, climatically matched habitat characteristics could impact the adaptive potential and population growth of an introduced species in their new range (Forsyth, Duncan, Bomford, & Moore, 2004; Hayes & Barry, 2008; Kolar & Lodge, 2001; Lodge, 1993). For Barbary ground squirrels, climate conditions of the source location (Sidi Ifni, Morocco; Machado, 1979; 133 mm rainfall/year and 19.2 °C, Merkel, n.d.) are very similar to the habitat on Fuerteventura

(Machado, 1979; <100 mm rainfall/year and ~ 20 °C, López-Darias & Lobo, 2008). Since the climate is so similar, it is no surprise that climate did not affect the squirrel's abundance in their invasive range (López-Darias & Lobo, 2008). Habitat preferences as well are similar between the native and the invasive ranges: distance to cultivated areas, distance to plant resources, and the amount of refuge/shelter, e.g., ravines, rock walls, stone heaps, and sandy soils, affect squirrel abundance in their invasive range (López-Darias & Lobo, 2008), while the presence of refuge and shelter and abundance of food resources are also predicting factors for the expansion of the Barbary ground squirrels in their endemic range (Rihane, El Hamoumi, El Agbani, Qninba, & Denys, 2018). Moreover, Barbary ground squirrels are reported to have a low diversity of parasites in their new range (López-Darias et al., 2008), and number of predator species (species richness) is lower in the invasive range (Gangoso et al., 2006; Medina et al., 2008) compared to the endemic range (Machado, 1979). As well, the main current aerial predator (the Eurasian buzzard) had an atypically small population at the time the squirrels were introduced (Gangoso et al., 2006), suggesting a release from predation around the establishment stage of the Barbary ground squirrel. Additionally, only 2% of the diet of the only terrestrial predator of the Barbary ground squirrel, feral cats, consists of the squirrels (Medina et al., 2008). Nevertheless, predation pressure may still be significant if the number of feral cats is large. No information regarding the population size of feral cats is available, but cats were introduced to the Canarian archipelago in the 15th century and are now present in each habitat of each main island (Medina et al., 2008). Overall, Fuerteventura can be considered a suitable habitat for the Barbary ground squirrel.

Barbary ground squirrels also may have become successful invaders due to behavioural advantages, as favourable behavioural traits promote success at each stage of the invasion (Carere & Gherardi, 2013; Chapple, Simmonds, & Wong, 2012; Holway & Suarez, 1999).

Species with increased interspecific or decreased intraspecific aggression, and behaviours enhancing their dispersal, e.g., exploration, activity, and boldness, should perform better in their new habitat (Holway & Suarez, 1999). These behavioural traits have been hypothesised to represent an invasion syndrome (Chapple et al., 2012; Sih, Bell, Johnson, & Ziemba, 2004), and can be linked to life history traits, which then result in “pace-of-life” syndromes (Réale et al., 2010). Often species with a fast pace-of-life syndrome, i.e., more explorative and bold species, have lower survival chances because they are more exposed to predators and parasites (Réale et al., 2010). For introduced species, a fast pace-of-life may be advantageous, since there are fewer predators and parasites resulting in higher survival chances. In Barbary ground squirrels, this hypothesis is supported, because more explorative individuals were better at avoiding predation, resulting in greater survival chances (Piquet, López-Darias, van der Marel, Nogales, & Waterman, 2018).

Finally, generalist species – species not specialised in habitat use or diet – are suggested to better adapt to a variable environment and to have a better chance of becoming successful than specialist species (Fisher & Owens, 2004). The Barbary ground squirrel has a generalist diet, because they are omnivorous and eat not only seeds, nuts, and fruits, but also native mollusks (López-Darias & Nogales, 2008; Machado & Domínguez, 1982). We have also recorded them feeding on the horns and hooves of goat carcasses (van der Marel, pers. obs.), supporting the suggestion that the squirrels could be mineral-limited (Machado, 1979). A generalist diet could also have helped the squirrels survive dry years with scarce resources, as they would have a wider niche breadth and not depend on a limiting resource. For example, in Darwin’s tree finches, generalist species have a more varied diet in dry years compared to wet years

(Christensen & Kleindorfer, 2009). Thus, multiple different aspects could have helped the squirrels overcome barriers in their introduced range.

Life history vs introduction effort in explaining invasion success of mammals and squirrels

None of the selected life history traits differed between invasive mammal species with a low introduction vs a high introduction effort measured as the number of locations introduced. At the introduction and establishment stage of the invasion, life history traits promote population growth and are predictors for success at these two stages (Allen et al., 2017; Capellini et al., 2015; Liu et al., 2017). Even at the spread stage, mammalian species have a greater chance of becoming invasive if they have larger, more frequent litters and a higher introduction effort (Capellini et al., 2015). Therefore, life history traits may not be important anymore for population growth once the species has successfully spread, because the population has already overcome the barriers that may have resulted in extinction risk during the three stages. Thus, life history traits that promote population growth do not differ between invasive species (species that successfully spread) irrespective of introduction effort. Apparently, other factors, similar to the factors mentioned above, such as habitat and other species characteristics, may be more important once successfully spread.

Invasive squirrels can be placed at the fast end of the “fast-slow continuum”, therefore a fast life history promotes their population growth at the different invasion stages. Additionally, introduction effort measured as the number of founders did not relate to invasion success of squirrels, instead life history traits, in particular reproductive lifespan, influence success at the spread stage. A long reproductive lifespan does not seem to fit a fast life history, but a long reproductive lifespan at the introduction stage means that introduced species have a higher

fecundity and can breed more often over a longer time span increasing the probability of overcoming extinction risk. At the establishment stage, a longer reproductive lifespan and larger litters promote population growth and consequently establishment success (Capellini et al., 2015). Hence, already at the introduction and establishment stage, species with a longer reproductive lifespan are selected for, and therefore, that trait may transfer to the spread stage. For invasive mammals in Australia, introduction effort explained success at the establishment stage, whereas life history traits were a more defining character for success at the spread stage, and climate suitability was important at both stages (Forsyth et al., 2004). Thus similar to these mammals, species and possibly habitat characteristics are more defining traits to explain expansion in the new range regardless of introduction effort.

It seems counterintuitive that introduction effort does not impact invasion success, because multiple advantages are associated with a high introduction effort (Blackburn et al., 2015; Colautti et al., 2006; Lockwood et al., 2005; Simberloff, 2009). First, multiple introduction events increase fitness (Keller & Taylor, 2010) and eventually genetic diversity (Dlugosch & Parker, 2008). Genetic diversity loss is U-shaped when plotted against time since first introduction, suggesting that an invasive population regains its genetic diversity over time, which can be promoted when multiple introduced populations connect (Dlugosch & Parker, 2008). Second, more founders reduce the risk of extinction and promote adaptability to the new environment through increased genetic diversity (Blackburn et al., 2015; Dlugosch & Parker, 2008). For example, lower genetic diversity caused by a small number of founders reduced the spread rate of grey squirrels (Signorile et al., 2014). Still, the species did successfully spread despite a low introduction effort, albeit slower, suggesting that a loss in genetic diversity does not imply a loss in the adaptive potential of an introduced species per se (Dlugosch & Parker,

2008). Instead, the probability for population growth from a small founding population in tree squirrels may be attributed to high reproductive output (Wood et al., 2007) or a fast life history. Additionally, climate suitability may be a better predictor for invasion success than the number of founders in squirrels, similar to mammals introduced to Australia (Forsyth et al., 2004). Normally, demographic stochasticity negatively affects population growth in small populations (Blackburn et al., 2015). However, other factors unrelated to demographic stochasticity, such as unsuitable habitat or climate, may negatively impact large populations as well (Blackburn et al., 2015). As such, small populations may then persist when other factors, such as climate and habitat suitability, work instead in their favour.

Concluding remarks and future studies

Barbary ground squirrels have a fast life history strategy resulting in rapid population growth. If these life history traits have not changed since 1965, their fast life history may have contributed to their invasion success with an extremely low introduction effort on Fuerteventura Island, as well as favourable behavioural traits, a generalist diet and good resources, enemy release, and similar habitats and climate. Only by understanding their basic biology will we be in the position to control and minimise the ecological damage this species causes in their new habitat. For a future study, we could run a population model to predict how long it would take for a pair of squirrels to spread across the island or to evaluate the necessary effort to control the population or reduce the number of squirrels on Fuerteventura, while taking the factors influencing their invasion success into account (Merrick & Koprowski, 2017).

Our study also aids in constructing a comprehensive framework on the factors, including life history traits, influencing invasion success. We found that life history traits do not differ

between successfully invasive mammalian species with a low or high number of introduction events, but a longer reproductive lifespan did relate to invasion success of introduced squirrel species irrespective of the number of founders. Thus, our results contradict the concept that introduction effort is the key factor influencing invasion success (Lockwood et al., 2005; Simberloff, 2009); instead, we argue that the invasion success can be influenced by multiple aspects of the new habitat or the biology of the introduced species.

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Table 2.1 A comparison of life history traits between mammals and species of the family Sciuridae (squirrels, including Barbary ground squirrels *A. getulus*) that successfully spread in their introduced range (invasive species)

	Mammals ¹			Only squirrels ¹				<i>U</i>	<i>P</i>
	<i>N</i>	mean	SE	<i>N</i>	<i>A. getulus</i> only	mean	SE		
Introduction effort	47	78.4	21.3	6	1	16.7	7.8	201	0.09
Body mass (g)	47	84053.0	26830.3	5	221.1	312.0	75.3	191	0.02
Neonatal body mass (g)	47	4780.8	1506.6	4	8.9	9.0	2.4	135	0.16
Litter size	47	3.2	0.3	5	2.9	3.5	0.6	99	0.57
Litters/year	47	1.9	0.2	6	1	1.5	0.2	138	0.94
Age at first birth (days)	45	503.3	56.5	5	344.8	339.7	17.0	128	0.63
Gestation time (days)	47	124.5	16.0	5	43.5	41.9	2.4	148	0.36
Weaning age (days)	45	100.1	14.2	5	66	54.9	7.6	133	0.52
Longevity (years)	47	19.5	1.8	5	5	14.9	2.7	147	0.37
Reproductive lifespan (days)	45	6484.8	1.7	5	1480.2	4803.4	3.2	139	0.42

¹ Life history traits adopted from Capellini et al., 2015, except for the Barbary ground squirrel (*A. getulus*) data.

Table 2.2 A comparison of life history traits between invasive mammals with a low (introduction effort < lower quartile; 9 introduction events, $n = 9$ species) and a high introduction effort (introduction effort > upper quartile; 50 introduction events, $n = 12$ species)

	Low introduction effort ¹		High introduction effort ¹		<i>U</i>	<i>P</i>
	mean	SE	mean	SE		
Body mass (g)	13182.3	7850.7	40579.3	20174.6	43	0.46
Neonatal body mass (g)	676.5	360.2	1688.2	776.3	38	0.28
Litter size	3	0.8	4.1	0.7	41	0.37
Litters/year	1.6	0.3	2.4	0.4	43	0.43
Age at first birth (days)	562.7	174.3	455	114.8	64	0.5
Gestation time (days)	86.7	28.2	95.6	26.4	46	0.6
Weaning age (days)	75.5	14	79.1	19.1	54	1
Longevity (years)	15.4	3.6	15.4	3.1	53	0.94
Reproductive lifespan (days)	4908.9	1247.8	5175.9	1030.3	51	0.86

Data of the species, other than *A. getulus*, were adopted from Capellini et al. (2015).

¹We recoded the continuous variable, introduction effort measured as number of introduction events, into a categorical variable based on the lower and the upper quartiles. We then used these quartiles to discriminate between species with a low and a high number of introduction events.

Table 2.3 AIC_c -model selection for our binary response variable of squirrel species that did not ($n = 23$ events for 8 species) and that did ($n = 61$ events for 8 species) successfully spread into their new geographical range

Model	K	logLik	AIC _c	delta	weight	R ² _m	R ² _c
Life history traits	5	-43.09	96.93	0.00	0.76	0.25	0.25
Global	6	-43.08	99.23	2.30	0.24	0.25	0.25
Null	2	-52.01	108.17	11.24	0.00	0.00	0.00
Founders	3	-52.01	110.30	13.37	0.00	0.00	0.06

The global model includes both the life history traits (litter size, litters per year, and reproductive lifespan) and number of founders as independent variables.

Table 2.4 Estimates (\pm SE), 85% confidence intervals, and odds ratios of the variables included in the model that best-supported whether a squirrel species did not ($n = 23$ events for 8 species) or did ($n = 61$ events for 8 species) successfully spread into their new geographical range

	Estimate	SE	85% CI	Odds ratio
<i>Intercept</i>	8.56	2.89	[4.80-13.36]	5223.90
Litter size	-1.15	0.46	[-1.87- -0.53]	0.32
Litters/year	-3.98	1.50	[-6.71- -2.23]	0.02
Reproductive lifespan	0.18	0.08	[0.08-0.32]	1.19

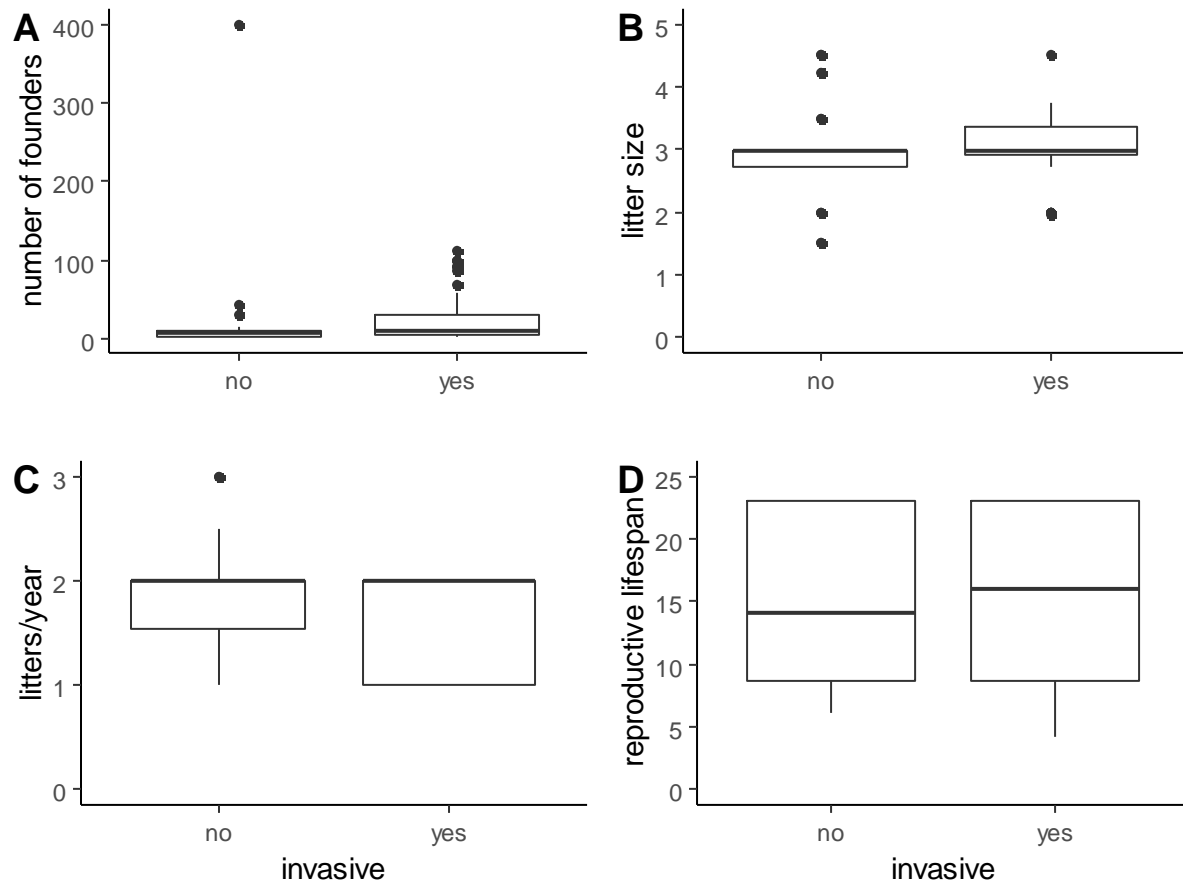


Figure 2.1 The (A) number of founders, (B) litter size, (C) litters per year, and (D) reproductive lifespan in years for squirrel species that did not successfully spread (no) and that did successfully spread (yes) into their new geographical range. The dark line is the median, the box edges are the upper and lower quartiles, while 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).

Chapter 3 Unique social organisation in a North African ground squirrel

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Author contribution

AM led the formulation of the research questions, hypotheses and study design, collected the data, performed the analyses and interpretation of the data, and wrote the manuscript. MLD and JMW contributed to the study design, assisted with data collection, provided feedback on the written manuscript, contributed to critical revision of the work, and supported this research both logistically and materially.

Abstract

Diurnal rodents living in harsh environments can be social to reduce the risk of predation. We studied this idea with the invasive population of the Barbary ground squirrel, *Atlantoxerus getulus*, on the arid island of Fuerteventura, Spain. Anecdotal accounts on their social organisation suggest them to be solitary, gregarious, or living in small family groups. We documented their social organisation using observational and genetic data. We hypothesised that females live in small matrilineal groups through natal philopatry (high within-group relatedness), whereas males are solitary and territorial, and are not related to other males within the site due to male-biased dispersal. Our data indicated that females live in all-female kin groups separate from adult males and unrelated adult males aggregated with subadults of either sex (individuals that have reached adult body size, are over six months old, but are not reproductive). We observed sex-biased dispersal with males being the dispersing sex and females mainly staying in their natal group resulting in more apparent kin structure in female groups than in male groups, but these results also suggest that kinship is not the only determinant of cooperation among the squirrels. Females sleep solitarily during gestation and lactation and either raise their litter communally or singly after juvenile emergence. In the non-mating season, male home ranges are larger than female home ranges and partially overlap female home ranges. During the day, males and females can be active in the same area where they mainly perform antipredator behaviour, foraging, or locomotion, but also show affiliative and agonistic interactions. The absence of hibernation and the presence of a breeding season may have resulted in the unique social organisation of Barbary ground squirrels – males sharing sleeping burrows with subadults of either sex – among ground squirrels. Understanding how kinship is related to this unique social

organisation is crucial to examining hypotheses relating to the costs and benefits that promote the evolution and maintenance of sociality.

Keywords: ground squirrels, group living, group size, invasive species, sexual segregation, sociality, social organisation, relatedness

Introduction

The spatiotemporal distribution of conspecifics and the social interactions among conspecifics helps to characterise a species' social system (Lacey & Sherman, 2007). For example, solitary species do not share space with conspecifics; species that form aggregations share space with conspecifics, but do not or rarely interact with another (Munroe & Koprowski, 2014; Parrish, Hamner, & Prewitt, 1997); and species that live in social groups share space and interact with conspecifics of different age and sex, e.g., having overlapping home ranges, performing social behaviours and communicating (sociality; Alexander, 1974; Armitage, 1981; Ebensperger, 2001; Hamilton, 1964a, 1964b; Silk, 2007; Wilson, 1975). Species, thus, vary along a continuum from solitary to cooperatively breeding species (Ebensperger & Cofré, 2001; Kappeler & Schaik, 2002). These differing levels of sociality are measured by studying the composition, cohesion, size and the genetic structure of a group, which are all part of a species' social organisation (Kappeler, 2019; Kappeler & Schaik, 2002).

Social species form groups via a variety of mechanisms. For example, groups may result from natal philopatry and delayed dispersal producing clusters of closely related individuals (Emlen & Oring, 1977; Greenwood, 1980). Non-mutually exclusive factors that may explain natal philopatry are ecological constraints and benefits of philopatry (Aguilera-Miller & Alvarez-Castañeda, 2019; Solomon, 2003). In mammals, dispersal is mostly sex-biased with males

dispersing farther from the natal area and females being philopatric, although female dispersal also exists (Greenwood, 1980; Mabry, Shelley, Davis, Blumstein, & Vuren, 2013; Wakefield, 2013). Consequently, females living in proximity to each other are often related and show kin-biased behaviour. Nevertheless, the genetic relatedness of individuals within groups is not the only factor contributing to aggregations and sociality. Non-kin groups can form if breeding is not limited to a dominant breeding pair (Lukas, Reynolds, Boesch, & Vigilant, 2005), if there are either high or low immigration and emigration rates with low or high survival, respectively (Davis et al., 2016; Matocq & Lacey, 2004), or if the sexes are segregated (e.g., one sex shows group formation by natal philopatry, while the other or both sexes show group formation related to other benefits, Ruckstuhl, 2007).

Benefits can accrue among kin through kin selection (Hamilton, 1964a, 1964b), and among non-kin through cooperative behaviour resulting from group selection (Mesterton-Gibbons & Dugatkin, 1992), reciprocal altruism (Axelrod & Hamilton, 1981) or byproduct mutualism (Mesterton-Gibbons & Dugatkin, 1992). For example, individuals in matrilineal kin groups may obtain direct fitness advantages via parental investment (Hare & Murie, 2007; Viblanc, Arnaud, Dobson, & Murie, 2010) and/or indirect fitness advantages related to kin-associated benefits (Dobson et al. 2012). However, when sharing space with conspecifics, social organisation or structure may be nonexistent (Munroe & Koprowski, 2014), and such aggregations can have both positive and negative effects on the fitness of the group members (Blowers, Waterman, Kuhar, & Bettinger, 2010). Thus, sociality is not only influenced by genetic constraints (Hamilton, 1964a, 1964b), but as well by phylogenetic (Sobrero, Inostroza-Michael, Hernández, & Ebensperger, 2014), life history (Armitage, 1981), or ecological constraints (Emlen, 1982).

Rodents play a major role in understanding the selective pressures that can lead to group living, because they vary widely in social organisation, from solitary to highly social species, and are widely distributed (Wolff & Sherman, 2007). Furthermore, they exhibit a wide array of species characteristics. Rodents can be diurnal, crepuscular, or nocturnal, and their lifestyle can differ among fossorial, semifossorial, arboreal, and semiaquatic lifestyles (Wolff & Sherman, 2007). These differences provide the potential for comparative studies to gain insight into the evolution of sociality. Sociality in fossorial old world hystricognaths species (a rodent infraorder) is hypothesised to be directly related to the harsh environment the species inhabits and the energetic costs of burrow excavation (Lacey & Wieczorek, 2003). For instance, in fossorial African mole-rats (Bathyergidae) higher levels of sociality occur in areas where burrowing is especially difficult, specifically in arid areas with hard soil, low and unpredictable amount of rainfall, and food resources that are patchily distributed (Lacey & Wieczorek, 2003). However, this pattern does not explain sociality in fossorial tuco-tucos (Ctenomyidae), where instead the heterogeneous distribution of suitable habitat explain their sociality levels (Lacey & Wieczorek, 2003; but see Tammone, Lacey, & Relva, 2012). Higher levels of sociality in new world hystricognaths are seen in diurnal species, in larger species, and in semifossorial species, e.g., degus, *Octodon degus*, and capybaras, *Hydrochaeris hydrochaeris* (Ebensperger & Blumstein, 2006; Ebensperger & Cofré, 2001; Ebensperger & Hayes, 2016).

Semifossorial rodent species living in arid environments (less than 250 mm annual rainfall, Maliva & Missimer, 2012) are mainly solitary and nocturnal, exploiting scarce and patchily distributed resources while conserving water, respectively (Randall, 2007). Although, some species of nocturnal desert rodents have also been observed to share burrows and nests (Santos & Lacey, 2011). Diurnal desert species often form groups through natal philopatry to

avoid predation and group members in these species show spatiotemporal overlap and social behaviours toward others (Randall, 2007). Some desert species show flexibility in their social organisation due to unpredictable environmental conditions, mainly rainfall. Rainfall affects desert rodent population dynamics due to the resource pulse that follows a precipitation event (Shenbrot, 2014), which influences population density and consequently habitat saturation. For example, in great gerbils, *Rhombomys opimus*, population densities are higher and social groups are larger in years with favourable environmental conditions compared to years with low amounts of rainfall (Randall, Rogovin, Parker, & Eimes, 2005). Habitat saturation (high population density) also favours group living in African striped mice, *Rhabdomys pumilio*, whereas reproductive competition favours solitary living (Schradin, König, & Pillay, 2010).

Levels of sociality in diurnal, semifossorial temperate ground-dwelling squirrels belonging to the tribe Marmotini (family Sciuridae) are suggested to be higher for ground-dwelling squirrels that experience high predation pressure, are larger in body size and absolute brain size, and have a short active season (Armitage, 1981; Blumstein & Armitage, 1998; Matějů et al., 2016; Michener, 1983, reviewed in Hare & Murie, 2007). This short active season can cause a delay in juvenile dispersal, because the squirrels live in a nutrition-deprived habitat due to environmental pressures (Armitage, 1981, 2017; Barash, 1974; Michener, 1983, 1984). Additionally, these harsh climatic conditions increase levels of sociality in sciurids, because some highly social species hibernate in groups, thereby deriving thermoregulatory benefits (Arnold, 1990). Thus, in temperate ground-dwelling squirrels, living in a harsh environment (long, cold winters) influences group living, but a short active season may not be relevant to explain grouping in ground-dwelling squirrels living in environments without this constraint.

The African ground squirrels (tribe Xerini) – a sister tribe to the temperate ground-dwelling squirrels – are diurnal, semifossorial rodents with a year-round active season (Happold, 2013). Thus, different selective pressures, such as a low and unpredictable amount of rainfall (Shenbrot, 2014) instead of a short growing season, may influence their social organisation. The extensively studied Cape ground squirrel, *Xerus inauris*, is social, with females living in matrilineal groups, while males associate with unrelated males to gain access to reproductive females that can come into oestrus year-round (Waterman, 1995). Although little information is available for the other species in this taxon, at least three of the five species appear to be solitary (Happold, 2013). The small amount of anecdotal information published for the small-bodied Barbary ground squirrel, *Atlantoxerus getulus* – the only species in the genus *Atlantoxerus* (Kryštufek, Mahmoudi, Tesakov, Matějů, & Hutterer, 2016) – suggests that they are gregarious (Machado, 1979), or that the group composition differs from being solitary to living in small (2-3 individuals) family groups dependent on the geographic region in the endemic range (Gouat & Yahyaoui, 2001).

We performed behavioural observations and genetic analysis on a population of Barbary ground squirrels to investigate to determine their social organisation. We hypothesised that Barbary ground squirrel females live in small matrilineal groups similar to the closely related Cape ground squirrels. Based on the few descriptions in the literature (Gouat & Yahyaoui, 2001; Machado, 1979), we predicted that female Barbary ground squirrels have a social organisation where there is spatiotemporal overlap of individuals and where affiliative interactions are present, but that males do not have overlapping home ranges and that they show agonistic interactions. We predicted that average relatedness within female social groups is not random and the observed within-female group relatedness is greater than expected by chance, while

relatedness among males is random and the observed relatedness does not differ from expected relatedness due to male-biased dispersal, i.e., relatedness among males within a site is low.

Methods

Species, study sites, and climatic data

We studied an invasive population of Barbary ground squirrels on the island of Fuerteventura, Canary Islands, Spain. The Barbary ground squirrel is active year-round, diurnal (Machado & Domínguez, 1982; van der Marel, López-Darias, & Waterman, 2019), small bodied (<250 g, Machado & Domínguez, 1982; Roth & Thorington, 1982), and has been suggested to be an obligate rock-specialist (Nutt, 2007). Since the first introduction of two individuals from Morocco to Fuerteventura in 1965 (Machado, 1979), the population has grown to an estimated million individuals and no additional introductions have been reported since the initial arrival (López-Darias, 2007).

Three study sites, differing in size and number of individuals (Appendix Table A1), were selected for this study (site 1: 28° 35' 58, 10" N–13° 59' 49, 15" W; site 2: 28° 35' 36, 81" N–13° 59' 48, 71"W; site 3: 28° 35' 38, 51" N–14° 00' 01, 41" W; Piquet, López-Darias, van der Marel, Nogales, & Waterman, 2018; van der Marel et al. 2019). The island and sites are characterised by ravines caused by erosion and numerous man-made rock walls and dams that fence properties and form terraces for land cultivation, respectively (López-Darias & Lobo, 2008). These rock structures function as shelter and lookouts for the squirrels (López-Darias & Lobo, 2008; van der Marel et al., 2019).

Fuerteventura is a volcanic island characterised by an arid climate (high temperatures ~20 °C and low rainfall, on average <100 mm/year) and semi-desert and rocky habitats similar to

their endemic range (López-Darias & Lobo, 2008; Machado, 1979). To characterise the climatic conditions of the island for the purpose of this study, rainfall data (mm) measured daily at the weather station of ICONA at La Oliva, Fuerteventura (approximately 7.1 km from our study sites) from October 1982 until May 2015 were requested from the island government.

Trapping and marking

We trapped Barbary ground squirrels in the mornings and afternoons approximately once a week from March through July 2014, January through July 2015, and January through June 2016 as these months encompass the breeding season. We trapped the squirrels with live traps (Tomahawk Co., WI, U.S.A; 13 x 13 x 40 cm) baited with peanut butter (McEneddy peanut butter, Lidl LLC, U.S.A.). In addition to checking the traps every 45-60 min, we covered the traps with cardboard and placed them strategically for the sun to minimise heat-induced stress. To reduce stress during handling, we transferred the squirrels into a conical handling bag (Koprowski, 2002). For individual identification, adult squirrels received a sterile 0.1 g 2.1 x 12 mm passive integrated transponder (PIT) tag (Avid Identification Systems, Inc., Norco, CA, U.S.A.) and a unique dorsal dye mark (Melchior & Iwen, 1965). Juveniles (individuals newly emerged from their nest burrow up to six months of age) received ear tags (#1005 Size 1 Monel, National Band and Tag Co., Newport, KY, U.S.A.) with differently colour-coded thread attached to their ear tags. Upon first capture, we also collected DNA samples (2-3 mm tissue of the tail tip stored in 95%-ethanol, Griffin et al., 2003). We determined the sex and age of the squirrels by looking at the swelling of the nipples for females and the development of the scrotum for males. Subadult males were those males that have reached adult body size, but have non-descended testes during the breeding season, while adult males have descended testes during the breeding

season. Subadult females were those females that have small nipples, as the nipples elongate and swell after their first successful parturition (Waterman, 1996).

Behavioural observations

To determine social organisation, we collected observational data during the same period as our trapping period. We used binoculars (Zwaluw 8 x 42, Vogelbescherming, The Netherlands) to observe squirrels from approximately 50 m from roads and nearby elevated areas. We collected observational data on squirrels from first emergence from their sleeping burrows until they immersed into their burrows again in the evening. The identity, location, and activities of all squirrels were recorded every ten minutes using scan sampling (Altmann, 1974). To record the observations, we used Numbers (Apple, Cupertino, CA, USA) and ‘Prim8’ software (McDonald & Johnson, 2014) on an iPod (Apple, Cupertino, CA, USA) and an Android phone (Motorola Droid A850), respectively. The specific behaviours recorded followed Waterman (1995) and are provided in Appendix Table A4. We recorded the locations of the squirrels using an adjusted Cartesian grid of ten by ten metres using the centres of the main rock walls or dams that crossed the site as our zero points. From those zero points, we marked every ten metres on the rock walls and other rock outcroppings in each wind direction with differently coloured spray paint (zero-points were coloured green and every ten metre point pink). We recorded the zero points in Universal Transverse Mercator (UTM) units with a GPS (Garmin GPSmap 78, Garmin International, Inc, Olathe, Kansas, U.S.A.) using the EPSG:4083 REGCAN95 / UTM zone 28N coordinate system, and thus referenced all other points in space using the Cartesian grid relative to those zero points.

Density and spatial and temporal overlap

We measured the size of the three sites by walking around the rock walls that bordered the ravines and stony plains with a GPS (Garmin GPSmap 78, Garmin International Inc., Olathe, Kansas, U.S.A.). The rock walls were considered the edge of the site as the ground squirrels rarely ventured out onto the stony plains, except for males during the mating season (van der Marel, pers. obs.). We established our field sites in 2014, but we increased the size of the sites in 2015 and 2016 to include more social groups. We estimated densities each year by dividing the number of adults by the size of the study sites, which we adjusted with the expansions.

To determine home ranges and home range overlap, we used the locations of both males and females from our 10 min scan samples outside of the mating season, only selecting individuals with more than 20 observations for final calculations. From March through August, the number of observations for males ranged between 23 and 303 observations, which we collected from March through August 2014. For females, we divided the post-mating period into two different periods: a pre-juvenile emergence (range 23-109 observations per female from March to May 2014) and a post-juvenile emergence period (range 21-182 observations from May to August 2014 and April to July 2015), because female African ground squirrels sleep solitarily with their offspring during lactation (Waterman, 2002). Home ranges were calculated using a kernel density estimator (Signer & Balkenhol, 2015; Worton, 1989). We used the reference bandwidth because it works best with clustered data (Signer & Balkenhol, 2015). For contour levels, we used a 50% contour level (hereafter kde50) to measure core areas and a 95% contour level (kde95) to prevent overestimation of the home ranges (Laver & Kelly, 2008). To calculate the kde95 overlap among females and males outside the mating season, we used the utilisation distribution overlap index (UDOI). This index measures home range overlap of two individuals

while taking the probability distribution of the individuals' space use into account (Fieberg & Kochanny, 2005). The UDOI index can range from 0% overlap (0) to more than 100% overlap (> 1), which may occur if there is substantial overlap between the utilisation distributions of two individuals and if their utilisation distributions are non-uniformly distributed.

We trapped sites regularly after juvenile emergence to measure either natal philopatry or dispersal of juveniles. Upon arrival the following field season, newly trapped individuals may have been some unmarked juveniles from the previous field season, because we were unable to trap all newly emerged juveniles before we left the field at the end of the summer.

Group size, composition, and cohesion

We defined a social group as individuals sharing sleeping burrows with one another, which is also used as social group definition in other semifossorial rodent species (Davis et al., 2016; Hayes et al., 2009). We included only observations with complete data of who entered (at night) or left (in the morning) the same burrow entrance during our behavioural observations. We measured the level of stability of the social groups (group cohesion) using an association index of individuals that shared a sleeping burrow for the night. We were unable to obtain calibration data, i.e., group and individual identification errors, therefore we used the simple ratio index (SRI, as suggested by Hoppitt & Farine, 2017). This index measures the proportion of time two individuals shared a sleeping burrow of the total time they were observed. The SRI varies from one (two individuals were always observed together) to zero (they were never observed together).

Throughout the day, patterns of group formation and sexual segregation might differ from the night (Radespiel, Sarikaya, Zimmermann, & Bruford, 2001). Therefore, we also calculated

the mean percentage of adult males and females in a 60 m radius within a 10 min scan using all our scan samples (van der Marel et al., 2019). For this analysis, we excluded days when females were in oestrus, because we changed to focal animal sampling on those days (although males and females were seen active in the same area on days of oestrus, van der Marel, pers. obs.).

Genetic structure

We extracted DNA from 189 tissue samples using the Chelex extraction protocol (Detwiler, Zajac, Minchella, & Belden, 2012). Microsatellite characterisation is described in Appendix Text 1. We excluded primers with error rates of over 50% or with potential null alleles ($n = 7$, Kratzer et al., unpubl. data) and individuals typed at fewer than 6 loci ($n = 4$). We genotyped our samples from 2014 ($n = 171$) using 11 microsatellite loci to determine kinship (Appendix Table A5). We used the program Genecap version 1.2.2 to check our dataset for double and problematic genotypes with the matching sibling probability set to lower than 0.05 (Wilberg & Dreher, 2004). We then performed a Pearson's correlation of observed and expected relatedness estimates using a simulated dataset of 1000 individuals with the same locus characteristics to assess the best of seven different estimators (Taylor, 2015; Van De Castele, Galbusera, & Matthysen, 2001; Wang, 2011): dyadic likelihood estimator (Milligan, 2003), lynchli (Li, Weeks, & Chakravarti, 1993), lynchr (Lynch & Ritland, 1999), quellert (Queller & Goodnight, 1989), ritland (Ritland, 1996), triadic likelihood estimator (Wang, 2007), and wang (Wang, 2002).

Time budget analysis

For a time-budget analysis, we selected adult ground squirrels that were observed for at least 50 minutes in at least five different observation periods (Edwards & Waterman, 2011). We excluded all occurrences sampling, days when females were in oestrus, and juveniles. We pooled the recorded behaviours for adult males and females separately into the following categories: 1) affiliative interactions; 2) agonistic interactions; 3) antipredator behaviour, i.e., vigilance and alarm calling; 4) foraging; 5) clean, i.e., autogrooming and sandbathing; 6) locomotion, including walking, loping, running and climbing; and, 7) sit with all four feet on the ground (following Waterman, 1995; Appendix Table A4). We measured individual time spent performing any of these behaviours as the number of scans when an individual was performing the corresponding behaviour divided by the total scans in which the individual was observed.

Statistical analysis

All statistical analyses were performed in R version 3.5.1 (R Core Team, 2017) unless stated otherwise. We used nonparametric tests if the assumptions of a normal distribution and homogeneous variances were violated. We reported the mean \pm standard error (*SE*) unless stated otherwise. We set our alpha to 0.05 for our statistical analyses. Figures were made with the R package ‘ggplot2’ version 3.0.0 (Wickham, 2009) and the ‘Survival’ package version 2.43-1 (Therneau, 2015; Therneau & Grambsch, 2000).

We performed Friedman’s tests to test for differences in densities across years per site and among sites per year. We used the ‘adehabitatHR’ package version 0.4.15 (Calenge, 2011) to measure home ranges and home range overlap. We log-transformed our home range estimates to meet the normal distribution assumption. As we only selected individuals with more than 20

observations, we did not have data per season for each year and each site. Therefore, we performed paired t-tests on our 50% and 95% kernel density estimator contour levels to test for size differences in female home ranges between the pre- and post-juvenile emergence period in 2014 and between male and female home ranges in the non-mating period. We performed the Kaplan-Meier approach on juvenile persistence within their natal site using the ‘Survival’ package version 2.43-1 (Therneau, 2015; Therneau & Grambsch, 2000).

For group size measurements, we combined the different group compositions. We tested for group size differences per season for males and females separately using a Mann-Whitney *U* test. To calculate the SRI of adult ground squirrels, we used the package ‘asnipe’ version 1.1.11 (Farine, 2018). We tested for SRI differences between sexes and among seasons using a generalised linear mixed model (GLMM) for a zero-inflated beta distribution using a zero-inflated beta regression in the package ‘gamlss’ version 5.1-2 (Stasinopoulos & Rigby, 2007). Males and the mating season were set as the reference values. We used site as our random effect. We visually inspected the model fit and we performed a likelihood ratio test between the model and a null model using the ‘lmtest’ package version 0.9-36 (Zeileis, 2002).

We used the package ‘Related’ version 1.0 in R version 3.4.1 for our relatedness estimation (Pew, Muir, Wang, & Frasier, 2015; R Core Team, 2017). We calculated ‘observed’ average relatedness within female and male social groups. We then generated ‘expected’ average relatedness values by shuffling individuals between groups using 1000 randomisation steps while keeping the size of the groups constant (Pew et al., 2015). If average relatedness within social groups was random, then observed relatedness would not differ from expected by chance. If average relatedness was not random, then observed relatedness would be greater than expected by chance. Next, we compared the observed relatedness between female and male social groups.

We log-transformed observed relatedness to meet the normal distribution assumptions and performed a two-sample t test. Finally, we performed a linear regression on average relatedness and adult group size.

As the measured individual time spent performing any of the specified behavioural categories (time budget) was zero-inflated and followed a beta distribution, we tested for sex differences per behavioural category using a zero-inflated beta regression in the package ‘gamlss’ version 5.1-2 (Stasinopoulos & Rigby, 2007). We used an interaction term between sex and behavioural category as our fixed factors and we used ID nested within site as our random factor. We used males and affiliative interactions as our reference values. We visually inspected our model fit. We presented the predictor estimates (β) \pm SE of the fixed factors and we performed a likelihood ratio test between the model and a null model for significance.

Results

Density and spatiotemporal overlap

Densities did not differ across years (Table 3.1; Friedman’s test: $\chi^2_2 = 2.00$, $P = 0.37$), nor across sites (Table 3.1; Friedman’s test: $\chi^2_2 = 4.67$, $P = 0.10$). Home ranges for both males and females were clustered around rock walls, dams, ravines, and abandoned cultivated areas. Both the core area (kde50) and the 95% contour (kde95) home range of females did not differ in size between the pre-juvenile emergence season (kde50: 2.78 ± 0.54 ha; kde95: 11.64 ± 1.89 ha, $n = 17$ for both) and the post-juvenile emergence season (kde50: 2.15 ± 0.36 ha, paired t test, $T_{16} = -1.59$, $P = 0.13$; kde95: 9.51 ± 1.26 ha, $T_{16} = -1.25$, $P = 0.23$, $n = 17$ for both). During the non-mating season, male home ranges (kde50: 3.01 ± 0.29 ha; kde95: 13.87 ± 1.71 ha, $n = 23$ for

both) were larger than female home ranges (kde50: 2.39 ± 1.77 ha, $T_{58.68} = 2.51$, $P = 0.01$; kde95: 10.43 ± 0.96 ha, $T_{46.41} = 2.61$, $P = 0.04$, $n = 42$ for both).

The utilisation distribution overlap index, which measures home range overlap while taking the probability distribution of an individual's space use into account, was $103.0 \pm 13.0\%$ within female social groups (Fig. 3.1, $n = 9$ female social groups excluding days of oestrus), and $88.0 \pm 13.0\%$ within male social groups (Fig. 3.1, $n = 5$ male groups). Male home ranges ($n = 41$ males) overlapped female home ranges ($n = 56$ females) by $17.0 \pm 3.0\%$ (Fig. 3.1).

Juvenile disappearance was highest within their first month of emergence (Fig. 3.2). Male juveniles disappeared from the site they were born in at a higher rate than female juveniles (Fig. 3.2; Kaplan-Meier approach: $P < 0.001$). After more than six months, no male juveniles remained at their natal site (Fig. 3.2). Of a total of 440 emerged juveniles, 5.2% ($n = 23$ males) were trapped and observed in a different site from their natal site on average 84.7 ± 6.1 days after first emergence. Almost all newborn females that survived into adulthood (41.7% of 204 emerged female juveniles were trapped the following field season) remained in the area they were born in (94.1% of $n = 84$), so five females dispersed to nearby areas. Upon arrival in the field the following field season, new captures were 64.0% adult or subadult males and 36.0% adult or subadult females ($n = 50$ newly trapped individuals).

Group size, composition, and cohesion

In the mating season, females shared sleeping burrows with 3.5 ± 0.3 [1 - 8] females ($n = 32$ burrow sharing events of 9 different social groups). After their day of breeding but before their parturition date, females isolated from their groups until juvenile emergence. Females varied in post-lactation behaviour because $58.8 \pm 5.2\%$ of the mothers moved their litter to a

communal burrow where they weaned their litters together with the litters of other females. On average 2.6 ± 0.2 [2-6] mothers and 8.7 ± 0.9 [2-25] juveniles were present in each group ($n = 33$ groups). Female group sizes in the mating season were larger than the female group sizes for communally breeding females (Mann-Whitney U test: $U = 3286$, $P < 0.001$). The mothers that did not join groups raised their litters singly (at least with their offspring) during the post-juvenile emergence period.

Males shared sleeping burrows with on average 3.4 ± 0.1 [1-16] individuals ($n = 545$ observed burrow sharing events). The majority of sleeping groups (76.9%) were comprised solely of adult males (2.7 ± 0.1 males, $n = 419$). Adult males were also observed to share sleeping burrows with adult females (total group size = 6.9 ± 0.5 individuals, $n = 55$), usually on days of oestrus ($n = 42$) compared to non-mating periods ($n = 13$), and with subadults of either sex during the non-mating period in 2014 (4.7 ± 0.3 individuals, $n = 71$), the only year we observed subadults (with the exception of one subadult in 2016; see Appendix Table A3). Over all three years, male group sizes were larger in the mating season (6.0 ± 0.4 , $n = 72$ burrow sharing events) compared to the non-mating season (3.0 ± 0.1 , $n = 470$ burrow sharing events; Mann-Whitney U test: $U = 25853$, $P < 0.001$). Throughout the day, male and female social groups were not always segregated, as we observed both adult males and females within 60 m in 50.2 ± 6.2 % ([41.8 – 62.2 %]; $n = 3$ sites) of our 10 min scans.

Group cohesion or SRI differed between the sexes and across seasons (LR test: $A = 140.5$, $P < 0.001$). Females' SRI (0.36 ± 0.01 , $n = 850$ associations in 12 social groups) was greater than the SRI of males (0.17 ± 0.01 , $n = 1291$ associations in 3 sites; estimate \pm SE = 0.82 ± 0.08 , $t = 9.78$, $P < 0.001$; Fig. 3.3A). Female SRI differed across seasons (mating season: 0.41 ± 0.01 , $n = 72$ females in 11 social groups; pre-juvenile emergence, but before the use of isolated

parturition burrows: 0.26 ± 0.03 , $n = 40$ females in 6 social groups; estimate \pm SE = -0.42 ± 0.10 , $t = -4.22$, $P < 0.001$; and post-juvenile emergence: 0.35 ± 0.02 , $n = 73$ females in 12 social groups; estimate \pm SE = -0.70 ± 0.12 , $t = -5.70$, $P < 0.001$; Fig. 3.3B). Male SRI did not differ between the mating season (0.18 ± 0.01 , $n = 59$ males in 3 sites) and the non-mating season (0.15 ± 0.01 , $n = 64$ males in 3 sites; estimate \pm SE = 0.003 ± 0.07 , $t = 0.04$, $P = 0.97$; Fig. 3.3C).

Genetic structure

Of the seven estimators that were described in the methods, the dyadic likelihood estimator (DyadML) showed the highest correlation between the observed and expected values of our simulated dataset (Milligan, 2003; Wang, 2007). Observed average relatedness (r) within female social groups ($n = 48$ females in 7 social groups) was 0.29 ± 0.06 , which was higher than expected from a randomly shuffled population ($P < 0.002$). However, when relatedness was independently analysed per group, two of the seven female social groups did not differ from random ($r = 0.19$ and 0.22 , $P = 0.12$ and 0.09 , respectively). The average relatedness within male social groups ($n = 46$ males in 6 groups) was 0.19 ± 0.02 , which was not higher than expected by chance ($P < 0.39$), and none of the male groups differed from random. Observed relatedness in female social groups was higher than in male groups ($t_{13,0} = -2.68$, $P < 0.02$). We found a negative relationship between female group size and average relatedness (linear regression: $y = 0.56 - 0.02x$, $R^2 = 0.55$, $P = 0.01$), but no relationship for males ($y = 0.27 - 0.01x$, $R^2 = -0.10$, $P = 0.49$). The relatedness was on average 0.23 ± 0.04 ranging from 0.00 to 0.74 for sleeping burrow associations of adult males and subadult females ($n = 4$ subadults from two different sites).

Time budget analysis

The time budget of the Barbary ground squirrels outside of the mating season differed per behavioural category (LR test: $\lambda = 857.3$, $P < 0.001$). Both adult males ($n = 38$) and females ($n = 60$) spent most of their time performing antipredator behaviour (vigilance and alarm calling), foraging, and walking or running. They spent less time resting without being alert (sit), autogrooming or sandbathing (clean), or interacting with conspecifics on days other than days of oestrus (Table 3.2, Fig. 3.4). Sex did not affect the time budget of the squirrels (Table 3.2, Fig. 3.4), but there was a trend toward females being more aggressive than males (estimate \pm SE = 0.43 ± 0.25 , $t = 1.70$, $P = 0.09$; Table 3.2, Fig. 3.4).

Discussion

The invasive population of Barbary ground squirrels is social, supporting the hypothesis that diurnal arid-adapted species can be social. Social patterns in female Barbary ground squirrels arise due to female philopatry, except during gestation and lactation when females sleep solitarily in isolated burrows. After juvenile emergence, females can adopt alternative tactics. The females will either raise their litter singly or communally with other mothers. Males disperse before they reach sexual maturity (Chapter 2). Contrary to our predictions that males are solitary and territorial, we found that unrelated adult males share sleeping burrows throughout the year and have overlapping male home ranges. Male home ranges are larger than and partially overlap female home ranges. After the mating period, males can share sleeping burrows with subadults of either sex (when present). After emergence from the sleeping burrows, male and female social groups can be present in the same area (< 60 m, van der Marel et al., 2019). Both males and females show affiliative and aggressive interactions, although the proportion of time spent

interacting is much lower than the proportion of time spent in antipredator behaviour, foraging, or locomotion. We conclude that the Barbary ground squirrel is social, because they share sleeping burrows, have spatiotemporal overlap, and show affiliative interactions.

We did not find differences in densities across years in our population of Barbary ground squirrels, even though rainfall patterns varied across years (Table 3.1). These results suggest that habitat saturation in the form of high population density may not impact sociality in Barbary ground squirrels the same as in other diurnal desert rodent species (Randall et al., 2005; Schradin et al., 2010). For example, for great gerbils and African striped mice good rainfall years result in high population densities, which then result in group living, as there is habitat saturation (Randall et al., 2005; Schradin et al., 2010). For the invasive population of the Barbary ground squirrel, even in good rainfall years, there is no shortage of sleeping burrows due to the vast amount of rock walls and dams, and the presence of old volcanic tunnels (López-Darias & Lobo, 2008). Therefore, a lack of density differences with varying levels of precipitation may be the result of the absence of habitat saturation. In years with low amounts of rainfall, group living in Barbary ground squirrels may still be favoured, because they lack territoriality. Additionally, other benefits, such as reduced predation risk, may outweigh the costs of group living in dry years.

Female Barbary ground squirrels nest in small matrilineal groups, which is often documented in mammalian species (Greenwood, 1980; Lukas & Clutton-Brock, 2011; Michener, 1983), suggesting that females may accrue both indirect and direct fitness benefits (Hamilton, 1964a, 1964b; Lacey & Sherman, 2007). However, as two out of the seven female social groups did not significantly depart from a random structure and some female juveniles dispersed to nearby areas, other factors, beyond kinship alone, may impact their social organisation. For example, the narrow-striped mongoose, *Mungotictis decemlineata*, has a dominance hierarchy

and in this species, only the juveniles of dominant females survive. Thus, female mongoose may benefit by dispersing to a vacant breeding territory (Schneider, Kappeler, & Pozzi, 2016).

Comparatively, dispersed colonial tuco-tucos, *Ctenomys sociabilis*, experience increased direct fitness compared to philopatric females, however group living is still favoured due to the constraints on dispersal (Lacey, 2004) and possible indirect fitness benefits accrued from staying in the natal group (Lacey & Wiczorek, 2004). Individuals may also accrue other benefits from leaving the natal group. For example, individuals may leave the site to avoid inbreeding or leave the natal group as the costs of staying in it, such as resource competition, reproductive suppression, male infanticide, or low dominance status, are too high (Clutton-Brock & Lukas, 2012). The factors influencing the decision for female juvenile Barbary ground squirrels to disperse are thus far unknown.

All pregnant females sleep solitarily in isolated/parturition burrows during gestation and lactation, which is common among ground squirrels (Michener, 2002; Waterman, 1996, 2002). After juvenile emergence, females were either observed to nest only with their offspring (40%) or to merge their litters with the litters of other females (60%). Thus, adult females appear to be facultative communal breeders, a behaviour that is common among rodents (Ebensperger, Hurtado, Soto-Gamboa, Lacey, & Chang, 2004; Hayes, 2000). Our results are in agreement with a study on the endemic population, where group structure varied during the reproductive season with females either singly or communally raising their litters (Gouat & Yahyaoui, 2001). These two tactics are also seen in great gerbils and African striped mice (Hill, Pillay, & Schradin, 2015; Randall et al., 2005). In female African striped mice, the adopted tactic depends on the availability of territories, the females' own body mass, and whether breeding is synchronised

with other group members (Hill et al., 2015), which may be potential explanations for the two observed tactics in female Barbary ground squirrels as well.

Male Barbary ground squirrels share sleeping burrows with unrelated males, because males disperse from their natal site before they reach sexual maturity (Chapter 2), which is typical for most mammals (Solomon, 2003). Multiple males have been observed to associate in black-tailed prairie dogs, *Cynomys ludovicianus*, but these males are usually related (Hoogland, 1981, 1986). Male eastern gray squirrels, *Sciurus carolinensis*, may form aggregations around females in oestrus (Koprowski, 1993). However, we found that male Barbary ground squirrel also lived in groups when females were not in oestrus. Possible benefits for same-sex relationships or associations of the dispersing sex are to reduce contest competition when a species has a linear dominance hierarchy with dominance being a predictor of the outcome (Lehmann & Boesch, 2009), or due to the spatial distribution of resources (Lehmann & Boesch, 2009; Wakefield, 2013). For Barbary ground squirrels, both benefits may influence male social bonds as there is a low rate of agonistic interactions and resources are patchily distributed. Additionally, aggregation of males might prove beneficial in the context of comparative mate choice, i.e., females may compare potential mates with the other males present in the group (Bateson & Healy, 2005).

Dispersed males not only associate with other adult males but also with subadults of either sex, especially during the period that pregnant and lactating females isolate themselves in parturition burrows. Our results suggest that the subadult females are either offspring or kin to some of the males they share their burrows with, although our sample size was low. These subadults are not always present, but unfavourable conditions, such as lower amounts of rainfall, could potentially influence the age of maturity as subadults were mainly present in the year with

the lowest amount of rainfall. In closely related Cape ground squirrels, multiple unrelated males also share sleeping burrows (Waterman, 1995, 1997), but dispersed males never grouped with females or subadults (Waterman, 1995). It is possible that year-round activity combined with the presence of a breeding season (as all adult females sleep solitarily in parturition burrows during pregnancy and lactation) in Barbary ground squirrels may have resulted in this unique social organisation.

We found that male groups are less cohesive compared to female social groups and male group composition fluctuated regularly throughout the year (low levels of simple ratio index), as cohesion did not differ during mating versus outside of mating. The social patterns of males may be similar to fission-fusion dynamics (Aureli et al., 2008). Fission-fusion dynamics are suggested to occur in species living in unpredictable or spatially heterogeneous environments (Sueur et al., 2011). Groups can split (fission) when the costs of group living become too high, and groups can merge (fusion) when the costs of group living are low (Couzin, 2006). For example, in chimpanzees, *Pan troglodytes*, and spider monkeys, *Ateles geoffroyi*, fission-fusion events are influenced by the abundance and the distribution of ripe fruit (Chapman, Chapman, & Wrangham, 1995). In giraffes, *Giraffa camelopardalis*, food distribution but also predation risk influences fission and fusion events (Bercovitch & Berry, 2010, 2013). For Barbary ground squirrels, the environment could be considered unpredictable in terms of the amount of rainfall and the timing of precipitation events. Furthermore, the environment can be considered heterogeneous as most food resources are clustered around the ravines, where the terraces for land cultivation were built, but then the food can be considered homogeneous within the terraces.

At night Barbary ground squirrels show sexual segregation by sharing sleeping burrows with individuals of the same sex, except when there are subadult females present or during days

of oestrous when occasionally both males and females were observed to enter and leave the same burrow entrance. Social sexual segregation is seen across the animal kingdom and different selective pressures, including social preference, differences in activity, burrow maintenance, predator avoidance, or avoidance of sexual harassment, have been suggested to explain this phenomenon (Romey & Wallace, 2007; Ruckstuhl, 2007; Ruckstuhl & Neuhaus, 2002, 2005; Schneider & Kappeler, 2016; Senior, Butlin, & Altringham, 2005; Waterman, 1995; Whiteside et al., 2017). Cape ground squirrels also show social sexual segregation (Waterman, 1995). In this system, male bands are suggested to persist year-round to reduce predation risk and to locate females in oestrus, because Cape ground squirrels do not have seasonal breeding, nor do females within groups breed synchronously (Waterman, 1996, 1997). We suggest that social preference, burrow maintenance, aggression, or predator avoidance could drive social sexual segregation in Barbary ground squirrels.

While Barbary ground squirrels mainly show sexual segregation at night, we observed that male and female social groups can be active throughout the day in the same area. Behaviour patterns throughout the day outside of the mating season were similar for males and females, although there was a tendency for females to have higher rates of aggression outside of the mating season compared to males. Low rates of male aggression have also been observed in Cape ground squirrels (Waterman, 1998) and woolly spider monkeys, *Brachyteles arachnoides* (Strier, 1992), and are hypothesised to be the result of year-round breeding and finding of females in oestrous (Waterman, 1998), or of ecological constraints and female choice (Strier, 1992), respectively.

Concluding remarks and future studies

We conclude that Barbary ground squirrels are social. Female social patterns arise due to female philopatry, while male grouping is influenced by male-biased dispersal. Even though sociality levels (solitary/asocial, single-family female kin clusters, female kin clusters/male territoriality, polygynous harems/male dominance, and egalitarian polygynous harems, Armitage, 1981; Michener, 1983) of temperate ground-dwelling squirrels are more continuous than categorical; Barbary ground squirrels do not fit this index, because of their year-round activity, the sharing of space by males and females throughout the day and their social segregation during the night. Further research is necessary to determine which selective pressures influence grouping patterns (e.g., group size and cohesion) in this species and to tease apart the reasons for the females to adopt alternative tactics. Social network analysis may prove a useful statistical tool to examine the social structure (dyadic interactions) of the Barbary ground squirrel in greater detail and to analyse the fluidity of their associations (Hartwell, Notman, & Pavelka, 2018; Lehmann & Boesch, 2009; Louis et al., 2018; Wakefield, 2013). Our research provides insight into the basic biology of the invasive population of Barbary ground squirrels, which is important to minimise the ecological damage this species causes in its new habitat and for their control. Furthermore, this study is only the second African ground squirrel species where sociality has been studied in detail and the only other one that is social. Therefore, our results contribute to the development of a comprehensive framework for the evolution of sociality in African ground squirrels.

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Table 3.1 Total amount of rainfall (mm) and number of adult and subadult Barbary ground squirrels (N) and their density (N/ha) per site and year on Fuerteventura Island, Spain

		2014		2015		2016	
rainfall		93.3		164.9		176.5 ¹	
site		<i>N</i>	N/ha	<i>N</i>	N/ha	<i>N</i>	N/ha
1	females	10	8.42	20	8.66	25	10.83
	males	13	10.94	14	6.06	16	6.93
	total	23	19.36	34	14.7	41	17.76
2	females	21	3.66	29	5.06	38	6.63
	males	14	2.44	24	4.19	24	4.19
	total	35	6.11	53	9.25	62	10.82
3	females	15	6.27	20	4.48	19	4.25
	males	13	5.44	14	3.13	16	3.58
	total	28	11.71	34	7.61	35	7.84
all	females	46	4.94	69	5.52	82	6.56
	males	40	4.30	52	4.16	56	4.48
	total	86	9.24	121	9.68	138	11.03

¹ Due to logistics at the biological station in La Oliva, the daily weather measurements stopped in October 2015. Therefore, archival rainfall data was taken from the website worldweatheronline.com accessed on 23 November 2018.

Table 3.2 Predictor estimates, standard error, and 95% confidence intervals for the activity budget characteristics (time spent interacting affiliatively or agonistically, cleaning, foraging, in locomotion, sitting, or alert) of adult males and females and between male and female Barbary ground squirrels on Fuerteventura, Spain

	Estimate \pm SE	95% CI
<i>(Intercept)</i>	-3.07 \pm 0.13	[-3.33 - -2.81]***
females	0.02 \pm 0.17	[-0.32 - 0.35]
agonistic	-0.21 \pm 0.20	[-0.60 - 0.19]
alert	2.65 \pm 0.15	[2.36 - 2.93]***
forage	1.26 \pm 0.15	[0.95 - 1.56]***
locomotion	1.56 \pm 0.15	[1.26 - 1.86]***
sit	0.29 \pm 0.18	[-0.06 - 0.64]
clean	0.08 \pm 0.18	[-0.27 - 0.43]
female:agonistic	0.43 \pm 0.25	[-0.07 - 0.92]
female>alert	0.04 \pm 0.19	[-0.33 - 0.40]
female:forage	0.02 \pm 0.20	[-0.37 - 0.41]
female:locomotion	0.00 \pm 0.19	[-0.38 - 0.39]
female:sit	-0.40 \pm 0.25	[-0.88 - 0.08]
female:clean	-0.08 \pm 0.24	[-0.55 - 0.39]

Males and affiliative interactions have been used as reference values in the zero-inflated beta regression. Significance level of $P < 0.001$ is denoted as ‘***’.

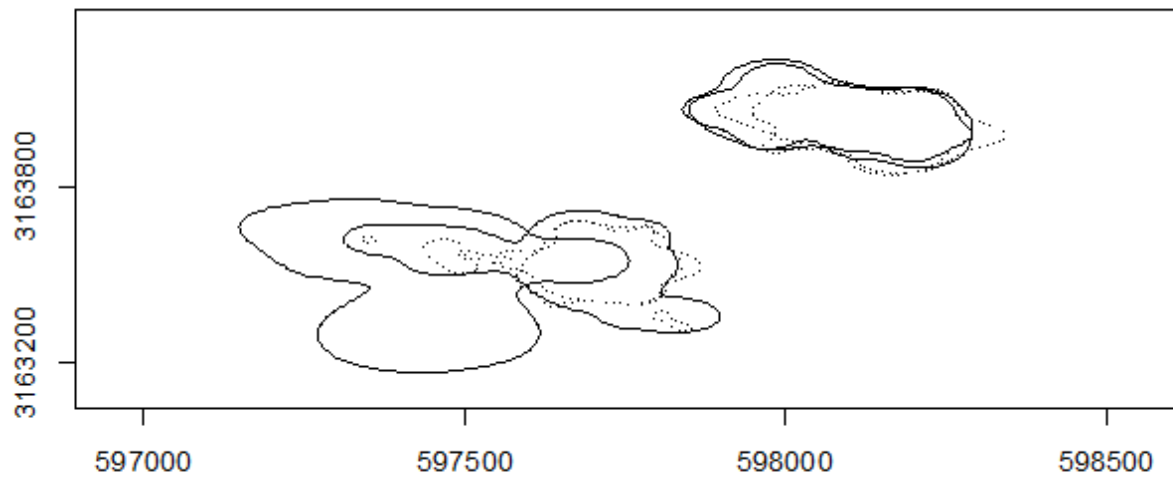


Figure 3.1 Home range overlap of the 95% kernel density estimator contour of a subset of Barbary ground squirrels in two different sites – four male (solid lines) and four female (dashed lines) – on Fuerteventura, Spain. Longitude in UTM is presented on the x-axis and latitude in UTM on the y-axis.

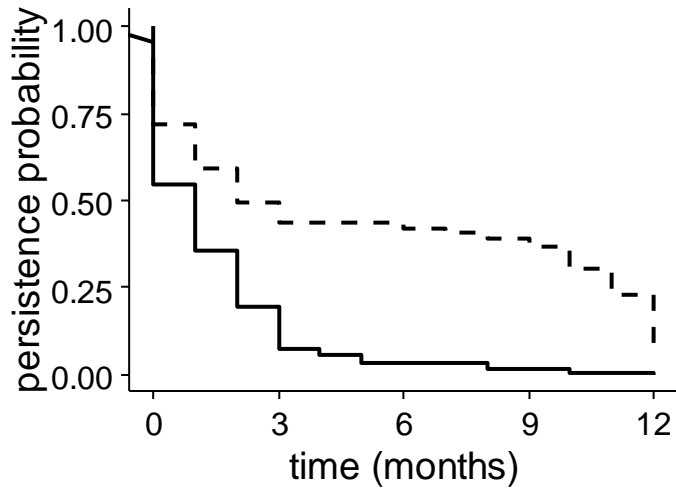


Figure 3.2 Persistence probability using the Kaplan-Meier approach of newly emerged female (dashed line) and male (solid line) juvenile Barbary ground squirrels within their natal site on Fuerteventura, Spain. First-year mortality in females is also shown, but not for males because they disperse from their natal site resulting in a steeper decline of persistence within the natal site for male juveniles ($P < 0.001$).

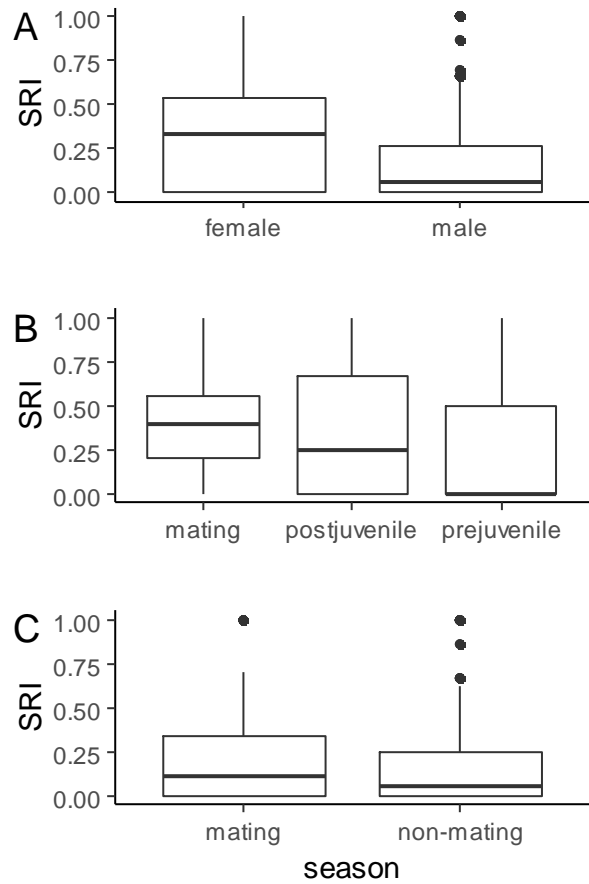


Figure 3.3 Simple ratio index (SRI) as a measure of group cohesion (A) between male and female Barbary ground squirrel' groups, (B) across seasons for female social groups, and (C) between the mating and non-mating season in male groups.

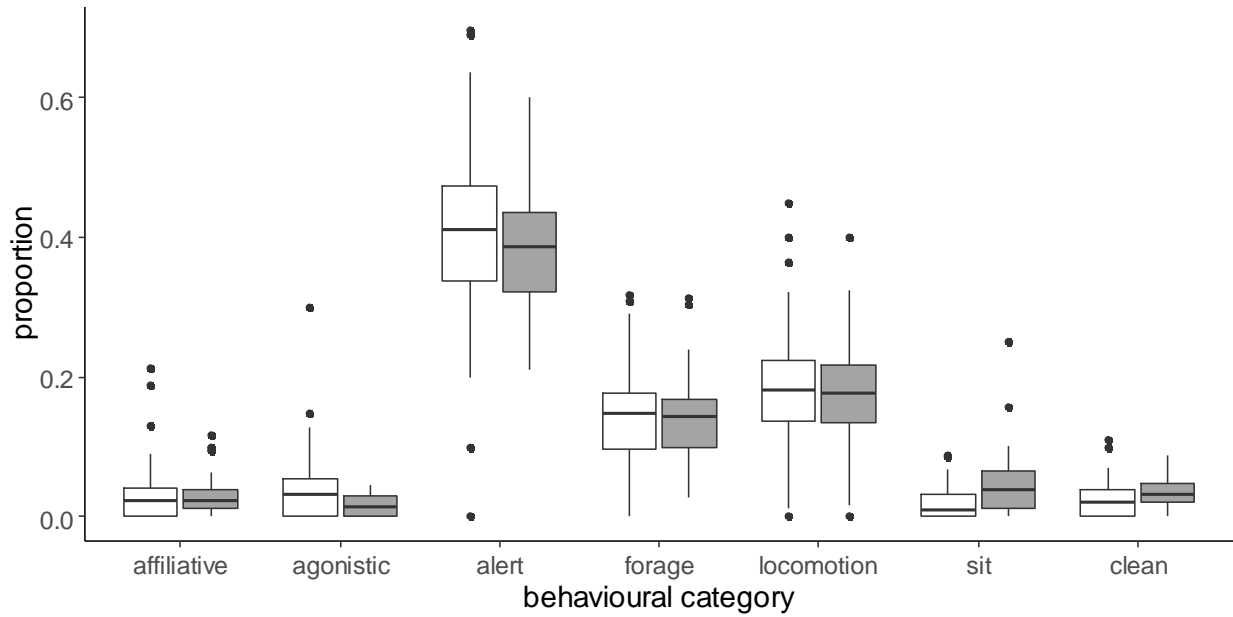


Figure 3.4 Boxplot of the time budget (proportion of time spent) of adult female (white; $n = 60$) and male (grey; $n = 38$) Barbary ground squirrels for seven different behavioural categories. Time budgets between females and males did not differ. The dark line is the median, the box edges are the upper and lower quartiles, while 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 quartile).

Chapter 4 Group-enhanced predator detection and quality of vigilance in a social ground squirrel

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Author contribution

AM led the formulation of the research questions, hypotheses and study design, collected the data, performed the analyses and interpretation of the data, and wrote the manuscript. MLD and JMW contributed to the study design, provided feedback on the written manuscript, contributed to critical revision of the work, and supported this research both logistically and materially.

Abstract

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 non-mutually 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.

Keywords: alarm calling, Barbary ground squirrel, collective detection, dilution effect, group size, quantile regression, vigilance

Introduction

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, Verburgt, & Bateman, 2009). Conversely, the trade-off between feeding

activity and predation risk may also affect the quality of foraging. Individuals may 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 organisation 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 vocalise (Machado, 1979), but whether these vocalisations are alarm calls to warn conspecifics of a 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 4.1.

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 semi-desert 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 characterised 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 minimise (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 minimise 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 minimise 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 A3). 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 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 the 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-ranks 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 generalised linear mixed model (GLMM) using the package ‘glmmADMB’ with the beta distribution and identity (ID) as a 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-ranks 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 (τ) 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 optimised 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 non-predatory 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 A6), 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 vocalisation, 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 ($\bar{X} \pm SD$) (see Appendix Table A6 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 was 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-ranks 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-ranks 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 4.2). Individual time spent in low-quality vigilance did not decrease for any of the quantiles with increasing group size (Table 4.2, Fig. 4.1A). 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 4.2, Fig. 4.1B). 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 4.2, Fig. 4.1C). 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 4.2, Fig. 4.1D).

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 4.3). 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 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. 4.2A), whereas the proportion of callers did not (Kruskal–Wallis test: $H_3 = 6.59$, $P = 0.09$; Fig. 4.2B). Call duration was longer for terrestrial predators compared to the ‘not observed’ call-eliciting source (post hoc test: $P < 0.001$; Fig. 4.2A), 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., 2007; 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 4.2). 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, & Reborada, 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-Darias & 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.

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; Rieucan 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 account. However, gaze direction would have been difficult to distinguish due to the eye position of Barbary ground squirrels, which are positioned on the side of their head, 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 riskiest 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., 2007), and synchronise 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). Synchronisation may occur because vigilance levels of group members convey the group's fear level ('contagion-of-fear' hypothesis) (Beauchamp, 2015b). Synchronisation 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). Synchronisation 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 vocalisation (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 et al., 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, more persistent 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 persistent 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 counterintuitive, 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 synchronised 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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Table 4.1 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 is conveyed in alarm calls	Duration of alarm calls will be longer in presence of a predator	Blumstein (2007); Warkentin, Keeley, & Hare, (2001)
	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.

Table 4.2 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	<i>P</i>	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
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	303.6			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 $P < 0.05$.

Table 4.3 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

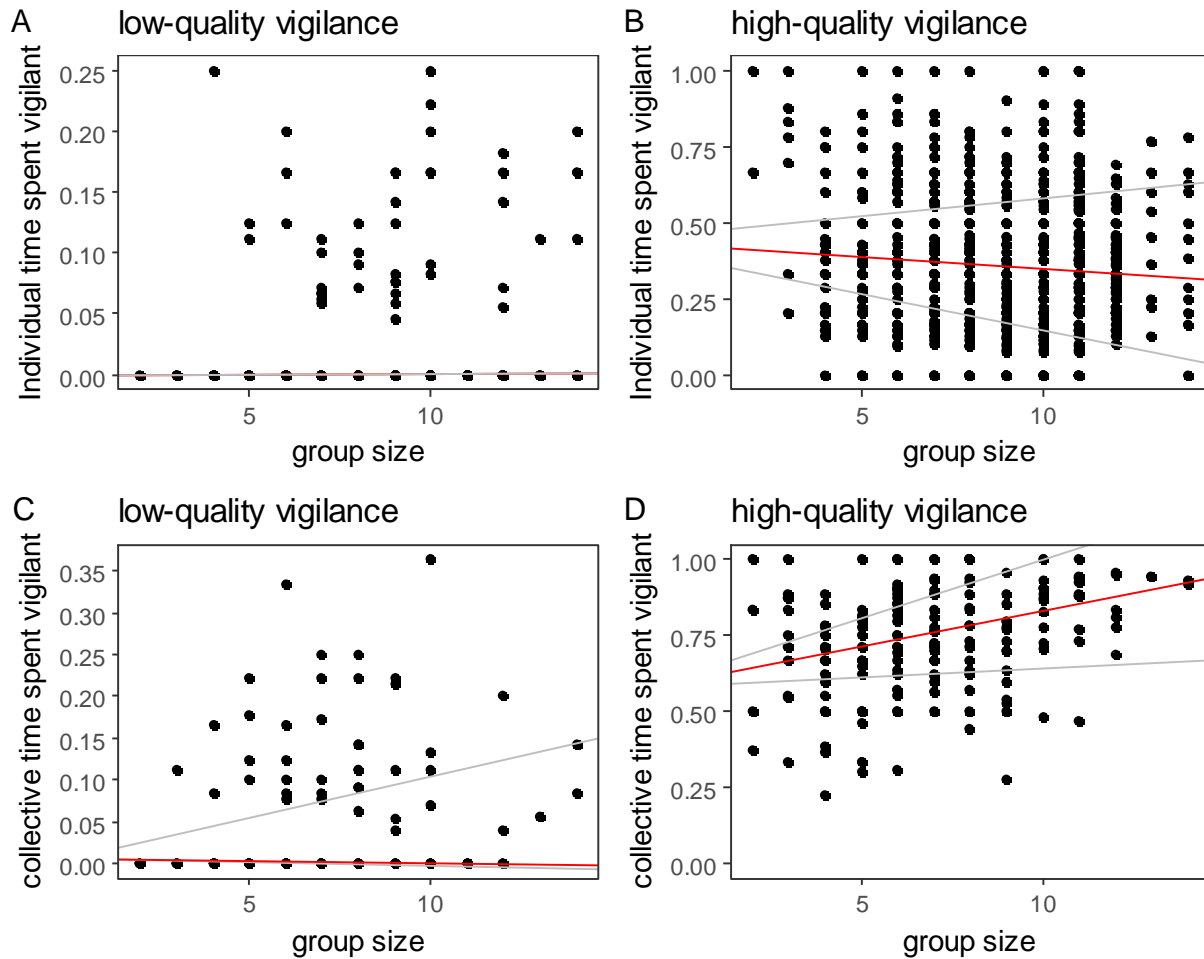


Figure 4.1 Quantile regression of individual (A) low-quality and (B) high-quality vigilance on group size, and of collective (C) low-quality and (D) high-quality vigilance on group size in Barbary ground squirrels. The solid grey regression lines represent the 0.2 and 0.8 quantiles, and the solid red regression line represents the 0.5 (median) quantile. Note the different Y scales for low- and high-quality vigilance.

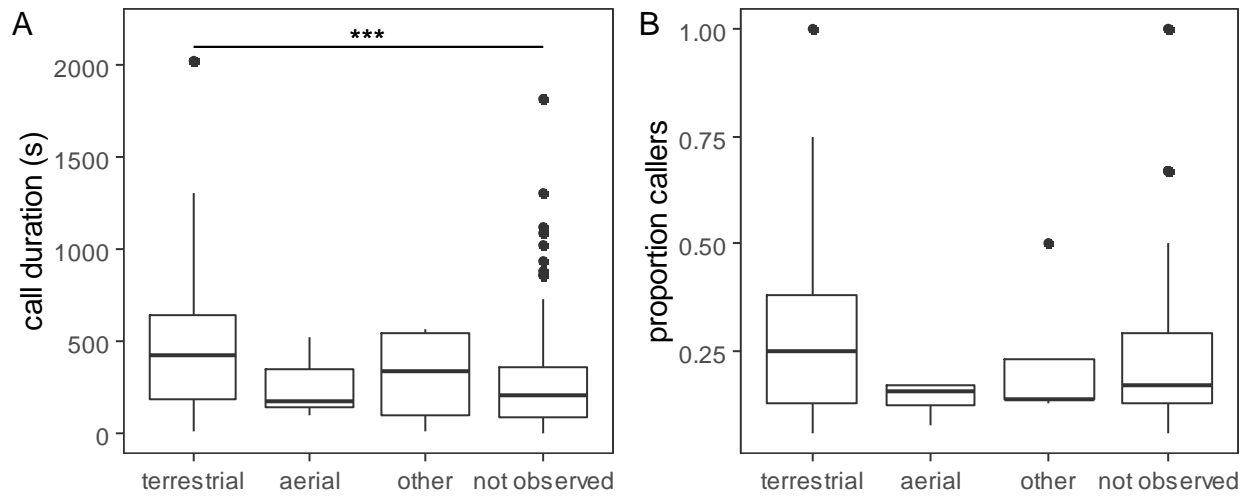


Figure 4.2 (A) Call duration and (B) proportion of callers for Barbary ground squirrels when aerial and terrestrial predators were present. The call-eliciting source ‘other’ included non-predatory heterospecific species. ‘Not observed’ refers to situations when predators or non-predatory heterospecific species were not observed. The 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 quantile). Significant differences are denoted by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Chapter 5 Information content of alarm calls in an invasive ground squirrel

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Author contribution

AM led the formulation of the research questions, hypotheses and study design, collected the data, performed the analyses and interpretation of the data, and wrote the manuscript. MLD and JMW contributed to the study design, provided feedback on the written manuscript, contributed to critical revision of the work, and supported this research both logistically and materially.

Abstract

Social species can use alarm calls to inform group members of danger. These alarm calls may contain information about predators or the urgency to respond. Variation in alarm calls may occur by combining different elements or by adding elements to the main syllables (affixation), which increases the effectiveness of the alarm calls. Selective pressures may influence a species' vocal repertoire, but these pressures may differ in geographically isolated populations. Our objective was to examine the response of the invasive population of Barbary ground squirrels to conspecific alarm calls in the field and to playbacks of manipulated conspecific alarm calls. We manipulated the alarm calls to test for affixation and whether the calls conveyed the urgency of the threat. In our observational study, we found that the proportion of vigilant group members and the average duration of vigilance increased upon hearing a conspecific alarm call elicited by a terrestrial predator compared to an unobserved threat. With higher wind speeds, the proportion of vigilant group members also increased upon hearing a conspecific alarm call. Adult females did not respond upon hearing the affix by itself or a control sound, but the squirrels showed a similar response to alarm call playbacks as to the naturally elicited alarm calls. Our results show that Barbary ground squirrels do not need an affix to convey information about a terrestrial threat, but to tease apart the function of the affix requires further research. The invasive population shows a response to novel predators, suggesting that they retained a generalised innate response from their native range, that at least some of their anti-predator behaviour may have evolved since their introduction, or that they learned their responsiveness to threats via associational learning.

Keywords: alarm calls, affixation, anti-predatory behaviour, Barbary ground squirrels, playback experiment, invasive species

Introduction

Collective detection of predators is one potential benefit of grouping in animals (Pulliam, 1973), where larger groups have a greater probability detecting predators in the environment in comparison to just one individual in solitary living species. For collective detection to work, at least one group member needs to be vigilant and communicate the threat to group members (Fairbanks & Dobson, 2007; van der Marel, López-Darias, & Waterman, 2019). The threat may be communicated via chemical signals as is seen in some aquatic species (Bairos-Novak, Mitchell, Crane, Chivers, & Ferrari, 2017; Smith, 1992), or through visual and auditory signals, e.g., by tail flagging (McRae & Green, 2014) or alarm calling (Klump & Shalter, 1984), respectively, in terrestrial species. These signals are thus critical for such a benefit of grouping to work.

Alarm-calling is one of the main signals used by birds and mammals to warn group members of danger (Klump & Shalter, 1984). Often, information within an alarm call is present to elicit appropriate behavioural responses in alarm call receivers (Evans, Evans, & Marler, 1993; Macedonia, 1990). The intended receivers are either conspecifics or predators. In the latter scenario, alarm calls may function as predator deterrents (Zuberbühler, Jenny, & Bshary, 1999). Alarm call playbacks can be performed to resolve whether the alarm calls actually function to communicate the threat to group members instead of as a predator deterrent (Kern & Radford, 2014).

When conspecifics are the intended receivers, anti-predator alarm calls may carry information about the situation, i.e., they may be functionally referential (Evans et al., 1993), or they may carry information about the motivational state of the sender (Evans et al., 1993; Macedonia, 1990). The latter reflects the urgency to respond to the predatory threat by

transferring, for example, information about the distance or direction of the predator (Macedonia 1990). Species living in open habitats have mainly one escape strategy of running away to burrows or bolt holes highlighting the importance to transmit the urgency to escape (Furrer & Manser, 2009; Harris, Murie, & Duncan, 1983; Macedonia & Evans, 1993; Waring, 1966). The urgency of the threat can be communicated through repeated calls and the parameter that conveys that information is the call rate (Warkentin, Keeley, & Hare, 2001). Other parameters that can vary – depending on the threat – are the number of callers (Blumstein, 2007), call type, duration of call bout, amplitude of calls, or other spectral properties (Manser, 2001; Warkentin et al., 2001). Species living in a more structured habitat have different escape strategies, including climbing a tree for a terrestrial predator attack or climbing down or into dense vegetation for an aerial attack. In these situations, functionally referential alarm calls transferring information about predator type or species are advantageous (Berthet, Neumann, Mesbahi, Cäsar, & Zuberbühler, 2018; Cunningham & Magrath, 2017; Evans et al., 1993; Macedonia, 1990; Manser, 2001). Alarm calls may also, instead of functioning solely as either referential or motivational, convey information about both (Manser, Seyfarth, & Cheney, 2002; Seyfarth & Cheney, 2003). Furthermore, both alarm call types may be present within a species, and individuals may use either a functionally referential or a motivational call depending on the predator context (Fichtel & Kappeler, 2002). Species may have different vocalisations (a different vocal repertoire) to convey information about the threat to group members.

The vocal repertoire is influenced by the anatomy of the species, as animal species are constrained in the production of different calls by their vocal tracts (Fitch, 2000). Therefore, species can combine different elements within a syllable or add a short element to the main syllable to increase their repertoire and change the meaning of the calls (Arnold & Zuberbühler,

2008; Collier, Townsend, & Manser, 2017; Jansen, Cant, & Manser, 2012; Sloan, Wilson, & Hare, 2005). Combining elements is also called segmental concatenation (Engesser, Ridley, & Townsend, 2016) whereas adding elements is called affixation (Ouattara, Lemasson, & Zuberbühler, 2009). To extract the potential function of segmental concatenation or affixation, alarm call playbacks may experimentally determine the receivers' response to these alarm calls.

Besides the anatomy of the species, a species' vocal repertoire can also be affected by different selection pressures, including social complexity, habitat characteristics, and predation pressure (Fischer, Wadewitz, & Hammerschmidt, 2017). First, the 'social complexity hypothesis' posits that species with greater social complexity evolved a more complex communication system (Freeberg, Dunbar, & Ord, 2012; Peckre, Kappeler, & Fichtel, 2019), which is supported in many ground-dwelling squirrels (Blumstein & Armitage, 1997b; Pollard & Blumstein, 2011, 2012), lizards (Ord & Garcia-Porta, 2012), and primates (Gustison, le Roux, & Bergman, 2012; McComb & Semple, 2005). Second, high winds increase anti-predator behaviour due to potential increased predation risk (Hollén et al., 2011), because wind reduces the signal-to-noise ratio of sound and consequently the ability to hear predators (Hayes & Huntly, 2005). Other weather variables, such as temperature and humidity, can also attenuate or degrade acoustic signals (Daniel & Blumstein, 1998). For example, higher temperatures increase the speed of sound, because hot air is less dense than cold air (Bohn, 1988; Goerlitz, 2018). Humidity increases the speed of sound because dry air is denser than moist air and sound can travel faster at lower densities/ higher humidity levels (Bohn, 1988). Weather conditions not only affect the speed of sound but atmospheric attenuation (absorption) of sound as well. Atmospheric attenuation is nonlinearly affected by temperature, humidity, frequency of sound, and pressure (Goerlitz, 2018). For example, the atmospheric attenuation of sound is greatest in the critical

range of relative humidity (10-40 %, Bohn, 1988). Thus, weather conditions may affect the probability that an individual calls or may affect the group response (Hayes & Huntly, 2005; Hollén et al., 2011). Third, predation pressure could influence the vocal repertoire or alarm communication in general, as predators could eavesdrop on signals transmitted by prey species (Deodhar & Isvaran, 2018; Rhebergen, Taylor, Ryan, Page, & Halfwerk, 2015). Prey species could also use multimodal signalling to communicate a threat. For example, Eastern grey squirrels, *Sciurus carolinensis*, use alarm calls to convey information about predator type, but they use multimodal signalling in the form of alarm calling and tail flagging to convey information about the threat (McRae & Green, 2014). Therefore, the ability to produce and convey different alarm calls is influenced by a species' vocal tract, social complexity, environmental conditions, and habitat characteristics, but for alarm communication to work the signal produced by an organism needs to invoke an adaptive response in another organism (Wilson, 1975).

The response to a stimulus or call is, besides the function of the call itself, also impacted by varying species characteristics, such as group size, presence of offspring, and behaviour of group members (Furrer & Manser, 2009; Le Roux, Cherry, Gyax, & Manser, 2009; Öst & Tierala, 2011). Mothers tend to increase their vigilance in the presence of offspring, as is seen in common eider females, *Somateria mollissima* (Öst & Tierala, 2011). A behavioural response of group members to an alarm call may include increased vigilance. Vigilance in response to a stimulus is also called 'induced' vigilance (Blanchard & Fritz, 2007; McDougall & Ruckstuhl, 2018). In the presence of lions (*Panthera leo*), plains zebras (*Equus quagga*) increase their induced vigilance, while impalas (*Aepyceros melampus*) do not, because zebras are the preferred prey of lions (Périquet et al., 2012). Furthermore, invasive species may have lost anti-predator

behaviours that were essential for survival in their endemic range but were unnecessary in their introduced range, because they have been separated from their ancestral predators in their new range, as described by the ‘enemy-release hypothesis’ (Keane, 2002; Torchin, Lafferty, Dobson, McKenzie, & Kuris, 2003). Thus, prey populations living in different geographically isolated areas, e.g., invasive and endemic ranges, may show different behavioural responses or may have lost a behavioural response (Chamaillé-Jammes, Malcuit, Le Saout, & Martin, 2014; Durand et al., 2012; Placyk, 2012).

Our aim was to study whether an invasive species has retained an anti-predator response to conspecific alarm calls using behavioural observations and a playback experiment. We used the invasive population of the Barbary ground squirrels, *Atlantoxerus getulus*, on Fuerteventura (Canary Islands, Spain) as our study system. Barbary ground squirrels have two different alarm vocalisations, a single whistle and a repeated bark (van der Marel et al., 2019). The single whistles can be considered productionally specific (Dezecache & Berthet, 2018) because mothers with newly emerged offspring emit them when an aerial predator attacks (van der Marel et al., 2019). The most common vocalisations are ‘repeated barks’ (van der Marel et al., 2019), which are repetitive calls (Collier, Townsend, et al., 2017; Owings, Hennessy, Leger, & Gladney, 1986) or tonic calls (Owings & Coss, 2007; Owings et al., 1986). These repeated calls are common alarm calls in ground-dwelling mammals (Blumstein & Armitage, 1997a; Davis, 1984; Manser, 2001).

We only focused on the repeated barks as alarm calls in this study, because the single whistles were only heard on three occasions (van der Marel et al., 2019). Although we artificially tried to elicit a response to both aerial and terrestrial stimuli, the ground squirrels were non-responsive to these stimuli. First, we analysed the behavioural response of group members

to conspecific repeated barks (observational study), and second, we performed a playback experiment (experimental study) to examine whether recipients respond similarly to a repeated bark in the absence of visual and other cues normally present in a predator context. For the playback experiment, we selected alarm calls emitted when a feral cat was present as feral cats prey upon the squirrels (Medina, López-Darias, Nogales, & García, 2008). We also manipulated the alarm calls to test for affixation as some alarm calls contain a brief element that precedes the main syllable (Fig. 5.1). The hypotheses and predictions are provided in Table 5.1.

Methods

Study site and subjects

Our study site was located in an area characterised by ravines, rock walls, xerophytic scrubland and abandoned cultivated areas (28°34'60" N, 13°58'0" W). The aerial and terrestrial predators in their invasive range are the Eurasian buzzard, *Buteo buteo insularum*, the common raven, *Corvus corax canariensis*, the common kestrel, *Falco tinnunculus dacotiae* (López-Darias & Lobo, 2008), and feral cats, *Felis catus* (Medina et al., 2008), whereas the number of different predator species is much higher in their endemic range (Machado, 1979).

Barbary ground squirrels are endemic to Morocco and were introduced to the island in 1965 (Machado, 1979). The scant information available on the social organisation of the Barbary ground squirrels suggests they are gregarious (Machado & Domínguez, 1982), although group composition may vary dependent on the reproductive stage they are in (Gouat & Yahyaoui, 2001). We found that males and females share sleeping burrows with on average three individuals of the same sex, but that both male and female social groups are observed to be active in the same area (within 60 m) throughout the day (Chapter 3). The population in our study site has previously been studied (for trapping details see van der Marel et al., 2019),

therefore all individuals were individually marked with a passive integrated transponder (PIT) tag (Avid Identification Systems Inc., Norco, CA, U.S.A.) and unique dorsal dye mark (Melchior & Iwen, 1965). We used live traps (Tomahawk Co., WI, USA; 13 x 13 x 40 cm) baited with peanut butter (McEnnedy peanut butter, Lidl LLC, U.S.A.) to trap squirrels.

Observational study: Response to alarm calls

From January through July 2014-2016, we recorded the response of group members within the caller's visible range (van der Marel et al., 2019) after an alarm call as 1) the average duration of high-quality vigilance of all group members, and, 2) the proportion of other group members performing high-quality vigilance. The alarm calls were elicited by terrestrial cats ($n = 29$ calls) or the eliciting call source was not observed ($n = 55$ calls). We defined high-quality vigilance as any vigilance bouts performed for more than 30 s and from promontories that were more than 30 cm in height (van der Marel et al., 2019). We recorded the weather variables, temperature ($^{\circ}\text{C}$), average wind speed (km/h), and humidity (%), twice a day with a Kestrel[®] 3000 Pocket Weather Meter (Nielsen-Kellerman, Boothwyn, PA, U.S.A.), and we recorded cloud cover on an ordinal scale. As we did not have a measure of the wind that coincided with each of the alarm calls, we took wind data from Tindaya, Canary Islands, Spain, which was approximately 2 km away from the study sites (www.worldweatheronline.com), that were closest in time to the alarm calls. The historical wind data was archived every three hours, therefore the time of the wind variable never differed by more than 1.5 hours from the time of the alarm calls.

We used a generalised linear model (GLM) with a gamma distribution to analyse the average high-quality vigilance duration of group members, whereas we used a GLM with a beta distribution to test for differences in the proportion of group members performing high-quality

vigilance upon hearing an alarm call in presence of a cat or a not observed threat using the package ‘Betareg’ version 3.1-1 (Cribari-Neto & Zeileis, 2010). We included the covariates following the hypotheses and predictions from Table 5.1. Covariates were group size, presence of juveniles, wind average, cloud cover, temperature, and humidity, as these variables could potentially influence the receiver’s response to an alarm call. We first tested for collinearity between our independent variables using the variance inflation factor (VIF) function from the ‘CAR’ package version 3.0-2 (Fox & Weisberg, 2011). None of our covariates had a VIF higher than three, therefore we included all independent variables (Zuur, Ieno, & Elphick, 2010).

We used information-theory using the sample size correction of Akaike’s information criterion (AIC_c) to select the model that best fit the data (Harrison et al., 2018). Models with a difference between a model’s AIC_c and minimum AIC_c (ΔAIC) of two or smaller were considered competitive (Burnham & Anderson, 2002). We then considered the most parsimonious model the best (Arnold, 2010). From the best-supported model, we presented the predictor estimates and the 95% confidence interval. We used the package ‘MuMIn’ version 1.42.1 (Barton, 2018) for our model selection, and residual diagnostics and the package ‘DHARMA’ version 0.2.0 to validate our models (Hartig, 2017).

Experimental study: Playback experiment

To perform the playback experiment, we recorded alarm calls opportunistically over a seven-month period in 2015. We started recording whenever we heard vocalisations for at least five minutes to make sure that the approaching observer was not causing the vocalisation. We used a Handy Recorder (model H4N; Zoom Corporation, Japan) on stereo setting to record the alarm call (<30 m to the caller) via the recorder's built-in microphones. Windy days were

avoided, as wind speeds exceeding 10 km/h are considered too strong for obtaining good recordings with a relatively high signal-to-noise ratio (Hare, 1998); thus sampling was limited as the average wind speed during our field seasons was 16.4 km/h ranging from 1 to 43 km/h. We were only able to record 26 alarm calls of 24 different adult females, even though all individuals emitted barks, and 17 of these calls had a signal-to-noise ratio between 7 and 50 dB (see Appendix Text A2 and Table A7 for a spectral analysis of these calls).

Of the 17 repeated bark calls with a good signal-to-noise ratio, we edited three different alarm calls (hereafter called “exemplars”), where the primary syllables of the alarm calls were preceded by a brief element (Fig. 5.1). We defined this brief element, hereafter called a first element or ‘chip’ as an affix to the alarm call. We selected the alarm calls containing the chip from three females from different social groups to avoid pseudo-replication (Kroodsma, 1989). We defined social groups as adult females sharing a sleeping burrow together (Chapter 2). We produced four 10 s long sounds or ‘playbacks’ from each exemplar: 1) an unaltered repeated syllable (alarm call complete, *acc*), 2) only the first element (the chip) of an alarm call syllable repeated (alarm call element 1, *ac1*), 3) only the second element of the alarm call syllable repeated, (alarm call element 2, *ac2*), and, 4) a white noise control (control, *c*). Following Makenbach et al. (2013), we produced three exemplars for the control with an amplitude of 26 dB and a total bandwidth of 22.05 kHz. We edited the exemplars and produced the control sounds using the software Praat version 6.0.37 (Boersma & Weenink, 2011).

We used only one adult female (focal ID) from each female social group ($n = 12$ social groups) for our playback experiments, as they have predictable sleeping burrow and foraging locations, making it easier to locate them compared to males. We used a random number generator (MS Excel 2013) to select the adult female from the group, the exemplar chosen for

each playback, and to determine the order of playbacks for each female (four playbacks per focal individual). We left at least a one-day gap between trials of the same female to prevent habituation (Shriner, 1998; Sloan & Hare, 2004). Prior to the playback, we recorded the behaviours of the squirrels present within the same area for 15 to 20 minutes to ascertain that the squirrels were at a low level of vigilance, defined as ‘not more than one individual being vigilant from raised positions and not performing any other behaviours’. If there was a high vigilance level (more than one group member performing high-quality vigilance), we observed the group until the group arrived at a lower vigilance level using 10 min scan sampling (Altmann, 1974). Once the focal individual was in sight, we positioned a speaker (Honeytone Mini Amp, Danelectro Co., Camarillo, CA, USA) at a distance of 28.9 ± 13.9 m (mean \pm SD, range 15 - 42.8 m). We recorded the behaviours of the focal female using focal follow sampling (Altmann, 1974). Once the focal individual was performing any behaviour other than vigilance after 10 to 20 minutes, we initiated the playback. We measured the decibel level of the calls using a digital sound level meter (model 407727, Extech Instruments Corporation, Nashua, NH, U.S.A.). The average decibel level of the playbacks was 60 dB SPL_C at a maximum distance of 43 m, which was similar to the average decibel level of an alarm call at a distance of less than 50 m (60 dB SPL_C, range 49-65 dB, $n = 3$). The same observer (AM) performed all playback trials (10 to 20 min preceding the playback, the 10 s long playback, and 10 min succeeding the playback), and recorded all behaviours using the application ‘Prim8’ (McDonald & Johnson, 2014) on an Android phone (Motorola Droid A850). We only performed trials when the wind speed did not exceed 18 km/h (Makenbach et al., 2013).

We investigated the individual’s response to the four playback sounds using generalised linear mixed models (GLMMs) for repeated measures (four playbacks per focal individual) fitted

by maximum likelihood. We set the control sound as the reference level for our analyses. We first measured an individual's response, measured as 'yes' when the focal was vigilant for > 10 s within 60 s after the playback using the 'glmerMod' of the 'lme4' package version 1.1-18-1 (Bates, Mächler, Bolker, & Walker, 2015) for the binomial distribution. We then measured the behavioural response. We considered individuals that increased their vigilance level from, for example, sitting posture to a standing posture as becoming more alert, and individuals that walked or ran toward cover and/or climbed to a lookout location to have a movement response. We used Cumulative Link Mixed Models (CLMMs) using the 'ordinal' package version 2018.8-25 (Christensen, 2015) to examine the strength of the initial behavioural response. We scored the initial behavioural response as: 1 = no reaction, 2 = alert, and 3 = movement (Collier, Radford, Townsend, & Manser, 2017; Hare & Atkins, 2001). We also measured the difference in the proportion of time spent vigilant one minute after minus one minute before playback using the 'lme4' package with a Gaussian distribution (Bates et al., 2015). Finally, we measured the latency to resume non-vigilant behaviour (any behaviour other than low- or high-quality vigilance) over a 10 min period using the 'lme4' package with a Gaussian distribution (Bates et al., 2015). We log₁₀-transformed the latency of the focal squirrel to resume non-vigilant behaviours because larger values could influence its correlation coefficients with other variables (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We used focal ID as our random effect and playback as our fixed factor. We used residual diagnostics to validate the models. We presented the predictor estimates (β) and the 95% confidence intervals of the fixed factor and we performed a likelihood ratio test between the model and a null model using the 'lmttest' package version 0.9-36 (Zeileis, 2002).

All statistical analyses were performed in R version 3.4.1 (R Core Team, 2017). Figures were designed in Praat version 5.4.06 (Boersma & Weenink, 2011) and the R package ‘ggplot2’ version 3.0.0 (Wickham, 2009).

Ethical note

All procedures conformed to ASAB/ABS's guidelines for ethical research with animals, were approved by the University of Manitoba Animal Care and Use Committee (protocol #F14-032), and were permitted by the government of Fuerteventura (Cabildo Insular de Fuerteventura #14885).

Results

Observational study: Response to alarm calls

First, we investigated the conspecific behavioural response to repeated barks. Model selection suggested that the model with call source best explained the average group vigilance duration (Table 5.2). The average group vigilance duration was longer when a call was elicited due to the presence of a cat compared to a call when the call-eliciting source was not observed (Table 5.3 and Fig. 5.2A). For the proportion of vigilant group members, the global model with all variables was the best fitting model (Table 5.2). Again, the proportion of vigilant group members was greater when a call was elicited due to the presence of a cat compared to a call when the call-eliciting source was not observed (Table 5.3 and Fig. 5.2B). Also, with higher wind speeds more individuals became vigilant upon hearing an alarm call (Table 5.3).

Experimental study: Playback experiment

Next, we examined whether recipients respond similarly to a repeated bark in the absence of visual and other cues normally present in a predator context. Of these calls, we selected the calls with the best signal-to-noise ratio from three different females. The repeated bark is a tonal vocalisation with a dominant fundamental frequency (Fig. 5.1). The frequency descends at the onset but stays flat after the major inflection point. Deterministic chaos (broadband noise) is present.

Females were vigilant for more than 10 s upon hearing the second element of the alarm call (*ac2*) and the complete alarm call (*acc*) compared to the control sound (*c*) but their initial responsiveness to the affix did not differ significantly among the three other sounds (LR test: $A = 14.23$, $P = 0.003$; Table 5.4 and Fig. 5.3). The behavioural response did not differ per playback (LR test: $A = 6.85$, $P = 0.07$; Table 5.4 and Fig. 5.3). Focal females spent more time performing high-quality vigilance after hearing the second element of an alarm call (*ac2*) and complete alarm call (*acc*) compared to the control (*c*) and the first element (*ac1*; Table 5. and Fig. 5.3; LR test: $A = 18.42$, $P < 0.001$). Finally, sound best explained the proportion log₁₀-transformed latency to resume non-vigilant behaviours (Table 5. and Fig. 5.3; LR test: $A = 13.54$, $P = 0.003$). Model validation indicated no problems.

Discussion

The responses to recorded alarm calls corresponded with responses when terrestrial predators were present. Group members became vigilant and were vigilant for longer when hearing a conspecific alarm call in presence of a terrestrial predator as opposed to an unobserved threat (observational study). Group members became vigilant more readily with higher wind speeds. As predicted, in the absence of a predator and upon hearing a conspecific alarm call

(experimental study), Barbary ground squirrels responded by becoming vigilant and by increasing their vigilance duration and their latency to resume non-vigilant behaviours. These results suggest that alarm calls of Barbary ground squirrels of the invasive island population warn group members of a terrestrial threat and/or that the alarm call initiates general alertness (Dezecache & Berthet, 2018).

The increase in latency to resume non-vigilant behaviours is similar to other bird and mammal species upon hearing a conspecific alarm call playback (Makenbach et al., 2013; Sloan et al., 2005; Yu et al., 2017), and the increase in vigilance bout duration is similar to the response of plains zebras in the presence of lions (Périquet et al., 2012). However, we did not find differences in the Barbary ground squirrel's behavioural response (i.e., changing to a more alert posture or moving to a burrow or vantage point) to the alarm call playbacks as compared to the control playback. Sometimes the movement response is scaled as a higher alarm level than adopting a more alert position (Makenbach et al., 2013). The movement in Barbary ground squirrels was to position themselves on rock walls instead of fleeing into a burrow, which differs from other ground squirrels that normally run to burrow entrances (Harris et al., 1983). The movement response, therefore, suggests that Barbary ground squirrels use their environment to gain a better viewpoint over their surroundings, which in turn can inform them about possible threats. The use of promontories by Barbary ground squirrels and their high-quality vigilance seems similar to the behaviour of sentinels, where individuals forego foraging and alternate their guarding bouts from raised positions (Bednekoff, 2015). Sentinel behaviour is seen in highly social species (Clutton-Brock, 1999; Ferguson, 1987; McGowan & Woolfenden, 1989; Rasa, 1986; Wright, Berg, Kort, Khazin, & Maklakov, 2001), but has never been recorded in rodents (Bednekoff, 2015).

Other factors that could influence an individual's response to alarm calls or playbacks are weather conditions (wind, temperature, cloud cover and humidity), group size, or the presence of offspring. However, neither the presence of offspring nor group size influenced the level of vigilance or duration of vigilance in the observational study. None of the weather variables, except wind speed influenced whether group members became vigilant after hearing a conspecific alarm call. Signal reliability may play a significant role in explaining the greater number of vigilant individuals for the population on Fuerteventura. 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. Wind can be considered an ambient noise that decreases the signal-to-noise ratio of sound (Bradbury & Vehrencamp, 1998), which can reduce the ability to hear predators (Hayes & Huntly, 2005; Hollén et al., 2011).

Finally, our results suggest that the second element is important, but that the affix (the 'chip') may not be necessary to inform group members of danger. Females increased their vigilance and latency to resume non-vigilant behaviours upon hearing the complete and second element of the alarm call, but not the affix (the 'chip') or the control sound. So, what is the function of the 'chip', especially because the 'chip' was only present in 36.4% of the recorded alarm calls? In Richardson's ground squirrels, about 67% of the alarm calls contain an affixation – an added element to a vocalisation, in this case, a trailing element after the main syllable – called 'chucks' (Sloan et al., 2005). This chuck serves to increase the vigilance level of call recipients. When chucks are included in whistle calls, it also directs the recipient's orientation to the caller (Sloan et al., 2005). Whistles are vocalisations produced in presence of terrestrial predators (Davis, 1984) or in situations where the threat is more persistent in comparison to immediate threats of avian predators (Sloan et al., 2005). Chucks are mainly included in these

whistles when the caller is close to a predator and perceives the threat as imminent (Sloan et al., 2005). We did not find that the vigilance level of Barbary ground squirrel receivers increased upon hearing the chip, but the chip might still function to direct the recipients' gaze to the caller. Male Campbell's monkeys, *Cercopithecus campbelli campbelli*, use affixation by adding the suffix 'oo' after the main syllable (Ouattara et al., 2009). This suffix alters the information content of an alarm call from a specific aerial or terrestrial predator to that of a general disturbance or alertness, respectively (Ouattara et al., 2009). In banded mongoose, *Mungos mungo*, the presence and structure of a suffix depends on the performed behaviour (Jansen et al., 2012). The chip in Barbary ground squirrels may alter the meaning of an alarm call in a way similar to the previously described species, but our methods were not sufficient to obtain the function or the subtleties of the context.

Concluding remarks and future studies

Barbary ground squirrels adjusted their behaviour according to perceived predation risk, suggesting that either meaningful information about the threat is conveyed and/or that the alarm call initiates general alertness (Dezecache & Berthet, 2018). The affix to the main syllable (the 'chip') is often absent in the alarm calls and does not convey information on the level of risk, i.e., females did not become vigilant or increased their latency to resume non-vigilant behaviours. However, it is unclear in what contexts the 'chip' precedes the second element of a repeated bark. Therefore, more detailed observations when recording repeated barks will be necessary, since it is difficult for human observers to hear whether the 'chip' is present in the alarm call. Additionally, ground squirrels are known to produce ultrasonic vocalisations (Wilson & Hare,

2006). Perhaps Barbary ground squirrel alarm calls have ultrasonic components that we could not pick up in our recordings.

Barbary ground squirrels have two different alarm vocalisations, a single whistle and a repeated bark (van der Marel et al., 2019), and it seems that the response of alarm call receivers differs per alarm call, suggesting that the alarm calls of Barbary ground squirrels also reflect urgency-responses similar to other ground-dwelling species (Macedonia & Evans, 1993; Manser, 2001). Although we artificially tried to elicit a response to both aerial and terrestrial stimuli, the ground squirrels were non-responsive to these stimuli. Therefore, we still have to explore this hypothesis. For example, with a greater sample size of the whistle alarm vocalisations, we could test whether the vocalisations 1) differ in their acoustic properties, 2) provoke a similar response when the eliciting predator is absent, or 3) elicit a different behavioural response (Evans et al., 1993; Farrow, Doohan, & McDonald, 2017).

Finally, our study shows that the invasive population of Barbary ground squirrels uses alarm calls to convey information about danger, which may simply reflect associational learning or may suggest that they retained a specific anti-predator response and that at least some of their anti-predator behaviour is innate or has recently evolved. However, to detect any differences in the invasive population's behaviour, we must further explore the alarm communication in both the invasive and endemic populations and the role that divergent environmental pressures play. Thus, further work will help us to understand the evolution of communication in ground squirrels and social mammals in general.

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Table 5.1 Hypotheses and predictions of the group members' response measured as the average duration of high quality vigilance of all group members and the proportion of other group members performing high quality vigilance upon hearing conspecific alarm calls elicited by terrestrial predators and the response to alarm call playbacks in Barbary ground squirrels on Fuerteventura, Canary Islands, Spain

Hypotheses	Predictions
Observational study: Response to alarm calls	
Group response to alarm calls depends on call source only	1) The group response will be higher upon hearing an alarm call when a terrestrial predator is present compared to an unobserved threat
Group response to alarm calls is influenced by social conditions	2) The group response will be higher with larger groups 3) The group response will be higher when juveniles are present
Group response to alarm calls is influenced by environmental conditions	4) The group response will be higher with higher wind speeds 5) The group response will be higher with lower temperatures 6) The group response will be higher with lower humidity and greater cloud cover 7) a combination of all weather conditions increases the group response to an alarm call
Experimental study: Playback experiment	
Squirrels glean information from calls in the absence of the visual stimuli of the predator	Upon hearing the alarm calls but not the control: 8) alarm call receivers become vigilant 9) move to an alert position or a better vantage point 10) increase their induced vigilance 11) increase their latency to resume non-vigilant behaviours
Squirrels use an affix to convey particular information	12) Squirrels respond differently to the affix in comparison to the control sound

Table 5.2 AIC_c-model selection for our response variables 1) the average duration of high quality vigilance of all group members, and, 2) the proportion of other group members performing high quality vigilance upon hearing conspecific alarm calls elicited by terrestrial predators or not observed threats in Barbary ground squirrels

Variables	K	logLik	AIC _c	delta	weight	R ² _m
Average group vigilance duration						
<i>source</i>	3	-626.09	1258.43	0	0.948	0.23
humidity + cloud cover	4	-628.36	1265.16	6.727	0.033	0.18
all variables	9	-623.47	1267.03	8.604	0.013	0.29
all weather variables	6	-628.25	1269.44	11.012	0.004	0.18
temperature	3	-632.69	1271.64	13.21	0.001	0.06
null	2	-634.7	1273.54	15.108	0	0.00
juveniles	3	-634.41	1275.08	16.647	0	0.01
wind	3	-634.65	1275.56	17.125	0	0.00
group size	3	-634.69	1275.63	17.203	0	0.00
Proportion vigilant group members						
<i>all variables</i>	9	85.17	-150.31	0	0.904	
source	3	75.8	-145.35	4.963	0.076	
wind	3	73.94	-141.62	8.689	0.012	
all weather variables	6	76.09	-139.27	11.045	0.004	
juveniles	3	72.36	-138.47	11.849	0.002	
null	2	70.72	-137.31	13.006	0.001	
temperature	3	71.31	-136.36	13.953	0.001	
group size	3	70.73	-135.21	15.104	0	
humidity + cloud cover	4	71.17	-133.92	16.397	0	

Models with values in italics are within two delta AIC values, while the models highlighted in bold best explained the data.

Table 5.3 Estimates and 95% confidence intervals of the parameters of the models that best-supported the average group vigilance duration and proportion of vigilant group members conspecific alarm calls elicited by terrestrial predators or not observed threats in

	estimates [95% CI]
Average group vigilance duration	
<i>intercept</i>	<i>0.002 [0.002 - 0.003]</i>
not observed call source	0.003 [0.002 - 0.005]
Proportion vigilant group members	
intercept	0.41 [-3.82 - 4.64]
not observed call source	-1.5 [-2.17 - -0.83]
group size	-0.06 [-0.14 - 0.02]
juveniles	0.44 [-0.13 - 1.01]
wind	0.07 [0.03 - 0.11]
cloud cover	-0.11 [-0.33 - 0.11]
temperature	-0.01 [-0.16 - 0.13]
humidity	0.0001 [-0.03 - 0.03]

The values in italic have confidence intervals excluding zeros.

Table 5.4 Coefficients and 95% confidence interval of the response of Barbary ground squirrels to each playback sound, only the first element of the alarm call (ac1), only second element of alarm call (ac2), and the complete alarm call (acc), which were repeated for 10 s

	individual's response ¹	behavioural response ²	Vigilance ³	log10(latency) ⁴
family	binomial	ordinal	gaussian	gaussian
<i>intercept</i>	-1.24 [-2.75 - 0.28]		0.07 [-0.11 - 0.26]	<i>1.23 [0.89 - 1.56]</i>
ac1	-0.38 [-1.69 - 0.92]		-0.01 [-0.20 - 0.17]	<i>1.77 [1.43 - 2.11]</i>
ac2	<i>1.79 [0.04 - 3.54]</i>		<i>0.39 [0.21 - 0.58]</i>	<i>2.23 [1.90 - 2.57]</i>
acc	<i>1.79 [0.04 - 3.54]</i>		<i>0.46 [0.27 - 0.64]</i>	<i>2.00 [1.66 - 2.33]</i>
none alert		-3.17 [-4.64 - -1.69]		
alert move		-0.001 [-0.58 - 0.59]		
(1 focal)	0.55	0.06	0.01	0.00

We also reported the distribution and the variance for the random effect (focal). The values in italic have confidence intervals excluding zeros.

¹ An individual's response, measured as 'yes' when the focal was vigilant for > 10 s within 60 s after the playback.

² The behavioural response (no reaction, alert, and movement response).

³ The difference in proportion time spent vigilant one minute after minus one minute before playback.

⁴ The latency (log-transformed) to resume non-vigilant behaviour over a 10-minute period after the playback.

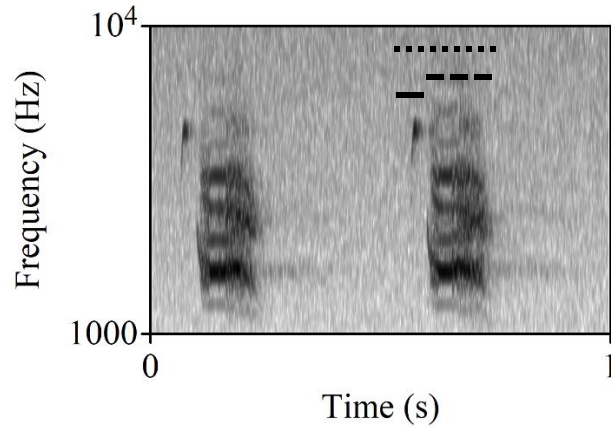


Figure 5.3 Spectrogram of a repeated bark with an affix of a female Barbary ground squirrel on Fuerteventura (Canary Islands, Spain). The dotted line corresponds to the duration of the complete alarm call, the dashed line corresponds to the duration of the second element, and the continuous line represents the duration of the first element. Spectrogram settings: Hamming-window, a Fast Fourier Transformation (FFT) length of 1024 with a 100% frame size, and 98.43% overlap.

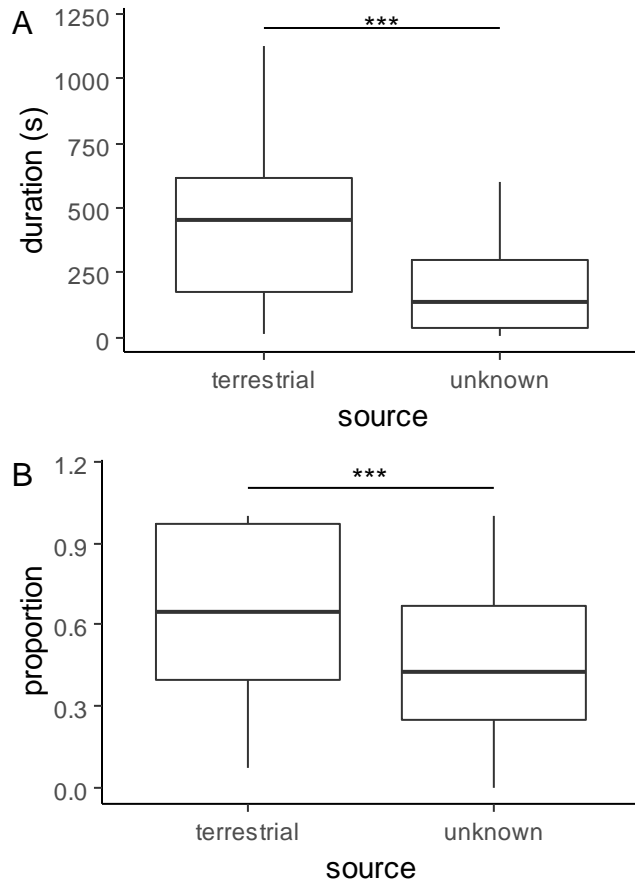


Figure 5.4 The model that best-supported (A) average group vigilance duration and (B) proportion of vigilant group members in Barbary ground squirrels included the call-eliciting source. Group vigilance duration was longer and proportion of vigilant group members was greater after hearing a conspecific alarm call elicited in the presence of feral cats (terrestrial) or when the human observer did not observe the eliciting call source (unknown).

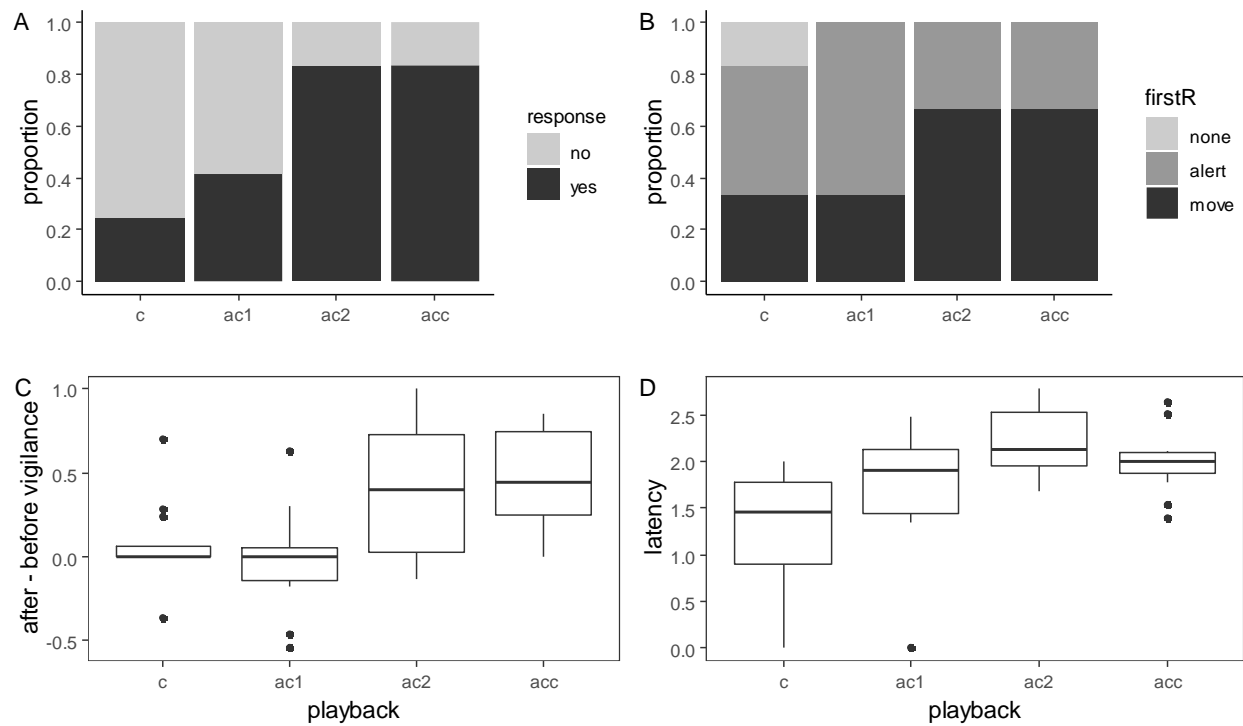


Figure 5.5 (A) Female Barbary ground squirrels’ response (measured as ‘yes’ when the focal was vigilant for > 10 s within 60 s after the playback), (B) behavioural response immediately after playback, (C) difference in proportion time spent vigilant 60 s after minus 60 s before playback, and (D) log₁₀-transformed latency to resume non-vigilant behaviour over a 10-minute period after the playback. The playbacks consisted of the control (c), the first element of an alarm call (ac1), the second element of the alarm call (ac2), and the complete alarm call (acc). The dark line is the median, the box edges are the upper and lower quartile, the whiskers are 50% from the median, and the closed circles are the outliers in figures 3C and 3D, calculated as the values smaller or larger than 1.5 times the box length (upper – lower quartile).

Chapter 6 Barbary ground squirrels on the qui vive: Sentinel or synchrony?

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Author contribution

AM led the formulation of the research questions, hypotheses and study design, collected the data, performed the analyses and interpretation of the data, and wrote the manuscript. MLD and JMW contributed to the study design, provided feedback on the written manuscript, contributed to critical revision of the work, and supported this research both logistically and materially.

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 behaviour) instead of high-quality vigilance (only performing vigilance) or 2) either by taking turns acting as sentinels or by synchronising vigilance bouts (vigilance coordination). Group members of species with a sentinel system are often closely related; however, the role of kin selection is not prerequisite to the evolution of such a system. To understand the importance of kinship in the evolution of coordinated vigilance, we set out to study coordinated behaviour and the effect of kin selection on this behaviour in a promiscuous species with lower levels of relatedness. The promiscuous Barbary ground squirrels, *Atlantoxerus getulus*, perform a type of vigilance ('perch behaviour') seemingly similar to sentinel behaviour as individuals performed high-quality vigilance at raised locations for over 30 s. We studied whether perch behaviour is coordinated and why the promiscuous Barbary ground squirrel performs this behaviour. Perch behaviour was not a sentinel behaviour instead it was synchronised. Both sexes performed perch behaviour, and individuals performed perch behaviour in absence and presence of kin and offspring. We found that survival or the amount of time spent foraging did not decrease for perched individuals, nor that personal survival increased. Our study adds to the growing literature on synchronised behaviour and allows us to further explore the function of collective vigilance, and demonstrates that the cost of the vigilance/foraging trade-off may not be high for this invasive species.

Keywords: anti-predatory behaviour, Barbary ground squirrel, invasive, sentinel, synchronisation, vigilance

Introduction

Diurnal prey species can avoid predation by investing in vigilance behaviour, which results in a trade-off with foraging (Bednekoff & Lima, 1998). Some species, including Cape ground squirrels, *Xerus inauris* (Unck, Waterman, Verburgt, & Bateman, 2009) and eastern grey kangaroos, *Macropus giganteus* (Favreau et al., 2015), can reduce the cost of the trade-off between vigilance and foraging by performing nonexclusive or low-quality vigilance, i.e., individuals are vigilant while performing another behaviour. Non-exclusive vigilance is often seen in habitats where the risk imposed by predators is relatively low. In riskier habitats with, for example, higher predation pressure, individuals will increase their time spent in exclusive or high-quality vigilance – vigilance without performing any other behaviour (Périquet et al., 2012; Unck et al., 2009).

Besides habitat risk and vigilance intensity, social conditions, including sex, age, and kinship, can also influence investment in vigilance. Males are often the sex that performs the most vigilance (Li et al., 2012; Pays, Sirot, & Fritz, 2012; Whiteside, Langley, & Madden, 2016), because of intraspecific competition (Reboreda & Fernandez, 2010) or mate protection (Horrocks & Hunte, 1986). Adults normally spend more time vigilant than juveniles (newborn sexually immature individuals), because juveniles will need to spend more time feeding in order to maintain a high growth rate (Lung & Childress, 2007; Pays et al., 2012). Thus, both social and environmental conditions influence investment in vigilance behaviour.

The cost of the trade-off between feeding activity and predator avoidance can also lead to the evolution of dependent vigilance within groups – individuals within the group coordinate their vigilance bouts – either by taking turns acting as sentinels or by synchronising their vigilance bouts (Beauchamp, 2015). Vigilance bouts are considered synchronised when

individuals are either vigilant or non-vigilant at the same time as their group members, which results in periods that either no group members or multiple group members are vigilant at the same time (Beauchamp, 2015). Synchronisation of vigilance bouts is frequent in both bird and mammalian species (Ebensperger, Hurtado, & Ramos-Jiliberto, 2006; McDougall & Ruckstuhl, 2018; Öst & Tierala, 2011; Pays, Dubot, Jarman, Loisel, & Goldizen, 2009; Pays et al., 2012; Pays, Jarman, Loisel, & Gerard, 2007; Pays, Renaud, et al., 2007; Podgórski et al., 2016).

Synchronisation 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), then the level of fear is heightened when other group members experience many vigilant neighbours as an indication of potential predation risk (Beauchamp, 2015).

Second, synchronisation can also arise when individuals benefit by detecting predators before their groupmates and can reach safety before other group members as predators target individuals that are last to find cover ('predators'-targeting-behaviour' hypothesis, Sirot and Touzalin 2009, Beauchamp 2015). As a third reason, multiple guards may be necessary to increase the collective view of the surroundings (Shackleton, Alves, & Ratnieks, 2018). Additionally, synchronisation may occur when individuals respond to the same stimulus, e.g., mimic vigilance bouts of group members that ceased chewing (McDougall & Ruckstuhl, 2018), or when group members synchronise feeding bouts (Beauchamp, 2015). Finally, group members may just be copying the behaviour of their nearest neighbour (Evans, Lihou, & Rands, 2018).

The cost of the foraging-vigilance trade-off can also lead to the evolution of sentinel behaviour. In species with a sentinel system individuals forego feeding and take turns performing high-quality vigilance from raised positions, which results in that one or two group members are always vigilant (Beauchamp, 2015; Bednekoff, 1997; Rasa, 1987). Sentinel behaviour is

observed commonly in some highly social bird and mammal species living or foraging in open arid habitats (Clutton-Brock, 1999; Ferguson, 1987; Manser, 1999; McGowan & Woolfenden, 1989; Newbold et al., 2008; Rasa, 1977; Wright, Berg, de Kort, Khazin, & Maklakov, 2001). The assumptions of a sentinel system are that sentinels warn group members of danger (Bednekoff, 1997), 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 also be located at raised positions or can alarm signal, Bednekoff (2015) argued that the main criterion of a sentinel system is the coordination of the high-quality vigilance bouts, which reduces the cost of the foraging and vigilance trade-off for group members. However, many species with a described sentinel system have actually not been tested for coordination (Bednekoff, 2015). A sentinel system may evolve because sentinels appear to be more effective at detecting predators due to their more focused vigilance and the elevated positions they adopt (Ridley, Nelson-Flower, & Thompson, 2013). Nevertheless, sentinel behaviour can be costly, as it is more likely to attract the attention of predators (Ridley et al., 2013). Sentinel behaviour may also be a cooperative behaviour (Santema & Clutton-Brock, 2013), where individuals gain fitness benefits through kin selection (sentinels only keep watch when close kin are present) or reciprocal altruism (Brandl & Bellwood, 2015; McGowan & Woolfenden, 1989; Rasa, 1987). Additionally, coordination of guarding bouts may be a necessity to divide the costs of being on guard over group members. For example, dwarf mongoose sentinels incur higher predation risk than non-sentinels (Ridley et al., 2013). Hence, the costs of vigilance are increased predation risk and/or less time available for foraging. Yet, sentinels may also be considered selfish when they are able to detect a predator earlier and reach safety faster than their group mates or when the decision to become sentinel is state-dependent (Bednekoff, 1997, 2001; Bednekoff &

Woolfenden, 2003; Clutton-Brock, 1999; Wright, Berg, et al., 2001; Wright, Maklakov, & Khazin, 2001). Most species with a sentinel system present stable social groups with high-relatedness among group members due to low levels of promiscuity (Fernández, Capurro, & Reboreda, 2003), suggesting that kin selection is an important mechanism for sentinel behaviour to occur. Although, Florida scrub-jays, *Aphelocoma coerulescens*, are also sentinel when nonkin are nearby (Bednekoff & Woolfenden, 2003). Thus, the role of kin selection in coordinated vigilance is not necessarily a prerequisite.

To understand the importance of kinship in the evolution of sentinel behaviour, it is essential to study coordinated vigilance in species where relatedness within groups varies, such as in promiscuous social species. The Barbary ground squirrel, *Atlantoxerus getulus*, an invasive species in one of the Canary Islands, is a highly promiscuous species (van der Marel, unpubl. data). Both males and females of this species position themselves on top of man-made rock walls (> 30 cm above ground) and actively scan the environment (> 30 s) without performing any other behaviour for approximately 40% of their daily activity budget (van der Marel, López-Darias, & Waterman, 2019). We termed this particular vigilance behaviour ‘perch behaviour’ 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, the perched individuals are the ones to alarm call to inform group members of danger (van der Marel et al., 2019; Chapter 5). Perch behaviour seems similar to sentinel behaviour, although the behaviour cannot be considered as a sentinel behaviour unless it is coordinated by individuals taking turns. Therefore, this species provides an excellent study system to examine coordinated vigilance in groups where relatedness varies.

Our objective was to investigate whether the Barbary ground squirrels coordinate their vigilance either by taking turns acting as sentinels or by synchronisation or whether perch behaviour is vigilance in response to an external stimulus, such as a predator, termed induced vigilance (Blanchard & Fritz, 2007). We also studied the social and environmental conditions, including sex, age, kinship, resource availability or predation pressure, that could influence perch behaviour in this species using the hypotheses and predictions presented in Table 6.1.

Methods

Study site

We studied an invasive population of Barbary ground squirrels less than 2 km west of Tindaya, 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, which are characterised by xerophytic scrubland and ravines caused by erosion (del Arco Aguilar, González-González, Garzón-Machado, & Pizarro-Hernández, 2010). The island is also characterised – as were all three sites – by dams and rock walls that were built to make terraces for land cultivation and to fence properties, respectively, and which function as shelter and perches for the Barbary ground squirrels to watch for predators (López-Darias & Lobo, 2008; van der Marel et al., 2019). The main predator of Barbary ground squirrels on Fuerteventura is the Eurasian buzzard, *Buteo buteo insularum* (Gangoso, Donázar, Scholz, Palacios, & Hiraldo, 2006). Other aerial predators are the common raven, *Corvus corax canariensis* (Gangoso et al., 2006), and the common kestrel, *Falco tinnunculus dacotiae* (López-Darias & Lobo, 2008), while the feral cat, *Felis catus*, is the only terrestrial predator (Medina, López-Darias, Nogales, & García, 2008).

Trapping, individual and group identification procedures

We trapped Barbary ground squirrels weekly using live traps (Tomahawk Co., WI, USA; 13 x 13 x 40 cm) baited with peanut butter. We did not trap when the ambient temperature was above 25 °C and we provided shade by covering the traps with cardboard to avoid heat stroke. Within 45 minutes of capture, we transferred squirrels to a conical bag for handling (Koprowski, 2002). Every adult squirrel was individually marked using a 0.1 g 2.1 x 12 mm passive integrated transponder (PIT) tag (Avid Identification Systems, Inc., Norco, CA, U.S.A.), while juveniles (individuals up to six months of age) received ear tags (#1005 Size 1 Monel, National Band and Tag Co., Newport, KY, U.S.A). Squirrels received a unique dorsal dye mark for individual identification at a distance (Rodol D, Lowenstein & Sons Inc., New York, U.S.A, Melchior & Iwen, 1965). We measured squirrel body mass using a spring scale (± 5 g; Pesola AG, Baar, Switzerland) and hind foot length (mm) using a Digimatic Plastic Caliper (Mitutoyo Corporation, Kawasaki, Japan), both as measurements for body size (Schulte-Hostedde, Millar, & Hickling, 2001). We evaluated the age of males and females following the descriptions in Chapter 2. We considered individuals in each other's visible range to be in the same social group (van der Marel et al., 2019). All methods 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.

Behavioural observations

To record perch behaviour of Barbary ground squirrels, we performed scan and all-occurrence sampling (Altmann, 1974). From 2014 until June 2015, we used the spreadsheet

program Numbers (Apple, Cupertino, CA, USA) on an iPod (Apple, Cupertino, CA, USA) to enter the behavioural data. From June 2015, we entered the behavioural data on an Android phone (Motorola Droid A850) using Prim8 Software (McDonald & Johnson, 2014). 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, Alexander, & Jovani, 2012; McDougall & Ruckstuhl, 2018).

To study perch behaviour in more detail, we also performed 10 min focal follows in 2015 (Altmann, 1974), recording focal follows for 81 individuals (range 1 to 7 focal follows per individual). Before sampling, we recorded site, focal ID, and ID's of all the individuals in sight within a 60 m radius (a squirrel's group, van der Marel et al., 2019). The order of observation periods among groups and sites and the order of focal follows was randomised using a random number generator (MS Excel 2013) or directly in the field using a randomiser application on an Android phone (Randomizer v. 0.2.6-beta, Mahé 2016), respectively. We only performed focal follows when no predators were observed to remove the possibility that individuals were responding to the same external stimulus (Beauchamp et al., 2012; McDougall & Ruckstuhl, 2018). During the focal follow, we recorded the behaviour, location, height of position, observations of other perched individuals, and the distance from the focal to cover.

Perch behaviour

We first provided the proportion of group members perched per scan excluding observations performed during the mating season. We analysed 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 & Zeileis, 2010) and the likelihood ratio test from the 'lmtest' version 0.9-36

(Zeileis, 2002). We then compared the proportion of perched individuals in our scan samples when a predator was observed or when we observed an alarm call (external stimulus present) *versus* 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 6.1). To test prediction 1 (Table 6.1), we used all observations and focal follows to determine the height of the location of perched individuals. We measured the height of the rock walls and dams that were used by the squirrels as promontories with a tape measure. We used a Mann-Whitney *U* test to examine differences in height between perched squirrels and squirrels that performed any other behaviour.

To explore predictions 2 and 3 (Table 6.1), we measured coordination of perch behaviour as the difference between the observed and expected proportions of time when at least one individual was perched per group (following Beauchamp, 2015; Öst & Tierala, 2011; Pays, Jarman, Loisel, & Gerard, 2007). We excluded days that females were in oestrus because male behaviour changed as they spent their time searching competitively for oestrous females, similar to what has been reported for the Cape ground squirrel (Waterman, 1998). We used all-occurrence data from our Prim8 input to measure coordination of vigilance using the exact duration of perch bouts (June and July 2015, February through June 2016). The Prim8 Software was useful to record the exact durations of perch bouts as we considered an individual to be perched when it was actively scanning the area from an elevated position of at least 10 cm above ground for more than 30 s without performing any other behaviour (Manser, 1999). 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 only used individuals that were observed for at least 50 minutes over a minimum of five observation periods (Edwards &

Waterman, 2011). We excluded unidentified individuals in our duration calculation because a different unidentified squirrel could have switched with the initial unidentified squirrel during a scan. Thus, start and end points of perch bouts could have corresponded to different unidentified squirrels. 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). Often the number of social groups are used as sample size, but we used the number of observation periods as our sample size, because multiple social groups may be interacting in the same area throughout the day (Chapter 3). Therefore, we assumed that 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 ($p_{\text{obs}} - p_{\text{exp}}$) 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 synchronised (Beauchamp, 2015). 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 behaviour and social conditions

To test prediction 4 (Table 6.1), we calculated activity budgets for perch behaviour and foraging of adults, subadults, and juveniles using our scan samples. We divided the number of scans where each individual was observed performing perch or foraging behaviour 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 behaviour (van der Marel et al., 2019), we tested for differences

among adults, subadults, and juveniles for males and females combined. Since our data were proportional and not normally distributed, we used Kruskal-Wallis tests to account for differences in proportion time spent in low-quality vigilance, perch behaviour and foraging from our scan data for adults, subadults, and juveniles, and among sites (prediction 4). If the results were significant, we performed post-hoc tests using a “Holm” correction (Holm, 1979).

To examine prediction 5 (Table 6.1), we collected tissue samples (2-3 mm tissue of the tail tip stored in 95%-ethanol, Griffin et al., 2003) upon first capture to determine relatedness in groups using 11 microsatellite markers (Chapter 3). We used the package ‘related’ to study the relatedness within groups (R package version 1.0; Pew et al. 2015). We first simulated relatedness of our population using 10,000 iterations and estimated the correlation coefficient of the seven relatedness estimators described in Chapter 3. We selected the relatedness estimator that showed the highest correlation coefficient (DyadML) in our study). We then used DyadML to estimate relatedness within the groups in the focal follows using 1000 iterations. Relatedness ranged from non-related ($r = 0$) to highly related ($r = 0.69$), but the average within-group relatedness was 0.19 ± 0.01 ($n = 191$ focal follows). We used generalised linear mixed models (GLMMs) with ID as the random factor for analyses where we had multiple measures for both our independent variables (alone vs in group, kin-selection, and parental behaviour) and dependent variable (proportion time spent perched). We used a ‘glmmADMB’ with the beta distribution (Bolker, Skaug, Magnusson, & Nielsen, 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; $r < 0.125$), but we used a Spearman’s rank correlation to test for a correlation between proportional time spent perched and relatedness of the group (prediction 5).

To test prediction 6 (Table 6.1), we used data from our focal follows to analyse whether perch behaviour was a parental behaviour. We analysed using glmmADMB whether adult females performed perch behaviour when their vulnerable offspring were present or absent (prediction 6).

Perch behaviour and survival

To test prediction 7 (Table 6.1), we recorded survival to examine whether animals that spent more time perching had lower or higher survival overall. We used our focal follows to record the distance to cover for individuals that were perched, feeding, or performing low-quality vigilance. We used only 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 individuals that were perched *vs* feeding. We also used the focal follows to test for a difference in perch behaviour when an individual was alone compared to when group members were present, which we analysed with a glmmADMB.

To test prediction 8 (Table 6.1), we considered individuals as survivors if the focal squirrels were trapped the following field season (2016). We also 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 in the different focal follows for analyses where we only had one measure per individual (survival, Julian date lived until, and age at disappearance). We used a Mann-Whitney *U* test to test 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). We performed a Spearman rank correlation on proportion of time spent perched and the last Julian date observed and a Kruskal-Wallis test on age at disappearance. We used our scan data to calculate the proportion of time that each squirrel allocated to foraging and perch behaviour, which we analysed 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, Schutz, & Hayes, 2014; Piquet, López-Darias, van der Marel, Nogales, & Waterman, 2018). We used the focal follows to test for a relationship between proportional times spent perched and body condition using a glmmADMB with ID as random factor (prediction 8).

All analyses were performed in R version 3.4.1 (R Core Team, 2017) and statistical significance was set to the level of 0.05. Unless otherwise indicated, averages are denoted as mean \pm standard error (SE).

Results

Perch behaviour

On average $42.5 \pm 1.2\%$ of a group was perched per scan ($n = 543$ scans), but we found no relation between number of perched squirrels and group size (Fig. 6.1). The percentage of individuals perched per scan when a predator was observed during the observation period ($50.6 \pm 1.2\%$, $n = 456$ scans) was similar to when no external stimulus was observed ($48.9 \pm 0.6\%$, $n = 2192$ scans; Mann-Whitney U test: $U = 525680$, $P = 0.08$; prediction 0).

Barbary ground squirrels were located at more elevated positions when perched (1.21 ± 0.02 m, $n = 2209$) compared to locations where the squirrels performed any other behaviour ($0.87 \pm$

0.02 m, $n = 5303$; Mann-Whitney U test: $U = 7724600$, $P < 0.001$, prediction 1) or low-quality vigilance (0.37 ± 0.04 m, $n = 234$; Mann-Whitney U test: $U = 449000$, $P < 0.001$).

We found that the proportion of observed time that at least one individual was perched, considering all individuals (0.19 ± 0.02) was smaller than the proportion of expected time for all individuals (0.54 ± 0.03 ; prediction 2; Table 6.2). Similar patterns were found for only adults or adult females (prediction 2 and 3; Table 6.2). We can call perch behaviour synchronised if the observed time is smaller than the expected time that at least one individual is perched in a group and if the difference between observed and expected proportions is smaller than zero. We found that the observed proportion was indeed smaller than the expected proportion that at least one individual in the group was perched (see above and Table 6.2), and the difference between proportions was smaller than 0 (prediction 2 and 3; Table 6.2).

Perch behaviour and social conditions

We did not find a difference in proportion of time spent perched among sites (Kruskal-Wallis test: $H_2 = 1.93$, $P = 0.38$), therefore we pooled our data across sites. We found differences among age classes for perch behaviour (prediction 4; Kruskal-Wallis test: $H_2 = 30.45$, $P < 0.001$). Juveniles spent less time perched ($24.7 \pm 2.6\%$, $n = 150$) than adults ($39.1 \pm 1.6\%$, $n = 157$; post-hoc: $P < 0.001$) or subadults ($34.2 \pm 1.5\%$, $n = 23$; post-hoc: $P < 0.001$), but there was no difference between adults and subadults (post-hoc: $P = 0.09$). We found no differences between age classes for time spent in low-quality vigilance (adults $2.1 \pm 0.7\%$, subadults $0.7 \pm 0.2\%$, and juveniles $1.4 \pm 0.8\%$; Kruskal-Wallis test: $H_2 = 3.12$, $P = 0.21$). Time spent foraging differed across age classes (Kruskal-Wallis test: $H_2 = 19.76$, $P < 0.001$): juveniles ($19.9 \pm 2.1\%$, $n = 86$)

foraged more than adults ($13.0 \pm 1.3\%$, $n = 96$; post-hoc: $P < 0.001$) and subadults ($13.4 \pm 2.8\%$, $n = 23$; post-hoc: $P = 0.01$).

Time spent perched did not differ when individuals performed perch behaviour in the absence ($33.5 \pm 3.6\%$, $n = 77$ focal follows) or presence of kin ($26.7 \pm 2.4\%$, $n = 114$ focal follows; GLMM: -0.35 ± 0.20 , $Z = 1.72$, $P = 0.09$, random factor: ID = 0.25; prediction 5). We also did not find a correlation between perch behaviour and relatedness (Spearman's rank correlation: $r_s = -0.05$, $P = 0.49$). Adult females ($n = 55$) spent a similar amount of time perched when vulnerable juveniles were absent ($32.4 \pm 2.7\%$, $n = 136$ focal follows) or present ($28.7 \pm 2.5\%$, $n = 102$ focal follows; GLMM: 0.12 ± 0.20 , $Z = 0.62$, $P = 0.53$, random factor: ID = 0.16; prediction 6).

Perch behaviour and survival

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). Individuals that were alone or in groups spent similar amounts of time perched ($37.3 \pm 5.2\%$, $n = 38$, and $29.5 \pm 2.0\%$, $n = 193$, respectively; GLMM: -0.19 ± 0.24 , $Z = -0.78$, $P = 0.43$, random factor: ID = 0.23; prediction 7).

We found no difference in survival, Julian day observed until, and age at disappearance with proportion of time spent perched (prediction 8; $n = 82$ 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). Foraging tended to be negatively correlated to time spent perched (prediction 8; Spearman's rank correlation: $r_s = -0.10$, $P = 0.08$), but performing perch behaviour

did not affect body condition (GLMM: 0.54 ± 1.10 , $Z = 0.49$, $P = 0.62$, random factor: ID = 0.09).

Discussion

We set out to study whether perch behaviour, defined as more than 30 s of long high-quality vigilance bouts more than 30 cm above ground, in a species with varying levels of relatedness is coordinated. We detected no relationship between the numbers of perched Barbary ground squirrels and group size. Furthermore, perch behaviour cannot be considered induced vigilance (Blanchard & Fritz, 2007), because perch behaviour was performed with equal frequency in the absence and presence of an external stimulus (a predator). Barbary ground squirrels met two criteria of a sentinel system: squirrels spend about 40% of the time perched from raised positions (van der Marel et al., 2019) and those on guard are the ones alerting group members of danger, as 78% of the observed alarm callers are positioned on promontories (van der Marel et al., 2019). However, Barbary ground squirrels did not take turns acting as sentinels as they never decreased the time between different perch bouts in a group. Instead, their perch bouts were synchronised because the observed time without a perched individual was smaller than the expected time resulting in a difference in proportions smaller than zero (Table 6.2). Finally, no apparent costs or benefits of perch behaviour at the individual or group level were detected.

Since it seems counterintuitive to be on the lookout at the same time as your group members, the question is why group members synchronise their perch bouts? First, the possibility exists that the decision of squirrels to perform perch behaviour is influenced by their internal state, i.e., perch behaviour may be an individual's optimal activity, as is seen in

suricates, *Suricata suricatta*, and Arabian babblers, *Argya squamiceps*, where individuals become sentinels when satiated (Clutton-Brock, 1999; Wright, Maklakov, et al., 2001). Barbary ground squirrels on Fuerteventura may be able to afford a reduction in their foraging behaviour as we did not find a relationship between perch behaviour and foraging or body condition, because of the resources available to the population on the island. Normally, herbivores are expected to spend a great proportion of their time foraging to meet their daily energy requirements (Fortin, Boyce, & Merrill, 2004) and often herbivores rarely stop chewing (McDougall & Ruckstuhl, 2018). But the herbivorous Barbary ground squirrels spend a surprisingly small proportion of their time feeding ($12.8 \pm 1.1\%$, van der Marel et al., 2019) in comparison to other species ($52.0 \pm 3.0\%$ in Cape ground squirrels, Unck et al., 2009; Waterman, 1995; 87% in Eastern grey kangaroos, G lin, Wilson, Coulson, & Festa-Bianchet, 2013; 64% in chestnut-crowned babblers, Sorato, Gullett, Griffith, & Russell, 2012; and 40% in Florida scrub jays, Fleischer Jr, Bowman, & Woolfenden, 2003). Hence, perch behaviour may be present because it may be an optimal activity when a squirrel is satiated and may imply that the trade-off between vigilance and feeding might be absent in this population of Barbary ground squirrels.

A second mechanism to explain synchronised vigilance in Barbary ground squirrels is the structure of the habitat because the presence of rock walls prevent them from looking on either side of the wall when on the ground. Therefore, to adequately detect predators, two individuals may be necessary to look in both directions of the rock wall. Hence, perch behaviour may simply be a form of extremely high-quality vigilance where individuals improve their level of detection by synchronising their 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 nest entrance to increase the view of their surroundings (Shackleton et al., 2018). Therefore,

similar to synchronised vigilance in the bees, squirrels may be vigilant at the same time on top of rock walls to watch ‘each other’s back’. Thus, the structure of the habitat (plains interspersed with ravines and rock walls) could influence synchronisation of vigilance in the Barbary ground squirrel.

As we used an observational study in the field, overall vigilance levels, distance between neighbours, group size, habitat, and social conditions could have affected levels of synchronisation. For example, when vigilance levels are high in a group, there is a greater chance that multiple individuals are vigilant at the same time, while for groups where vigilance is overall low, there is less chance of detecting synchronisation (Beauchamp, 2015). Other factors that could affect level of synchronisation are increased distances among neighbours (Pays et al., 2009) because it will be too difficult to monitor neighbours that are too far away or group members in larger groups (Beauchamp, 2015). Finally, social conditions, including sex, age, kinship, or being a parent, may influence perch behaviour. Barbary ground squirrel males and females spent the same amount of time perched (van der Marel et al., 2019), therefore there is no sex-biased benefit perching, suggesting that perch behaviour does not serve a function in intrasexual competition (Walker, York, & Young, 2016) or in mate protection (Horrocks & Hunte, 1986). Adults and subadults performed more perch behaviour than juveniles, which is similar to other bird and mammalian species (Ferguson, 1987; Rasa, 1977). Neither did kinship influence who was on perch duty, because individuals were perched independent of whether close kin were in their visible range or not. We found differences in relatedness among individuals (Chapter 3), even though we studied an invasive population most likely founded by only two individuals (Machado, 1979). The varying levels in relatedness suggest that the population has regained genetic diversity, which is possible if the founders reproduced quickly

after their introduction (Nei, Maruyama, & Chakraborty, 1975) and, which is likely because the squirrels have large and frequent litters promoting population growth (Chapter 2). Lastly, Barbary ground squirrels were perched in the absence and presence of juveniles, refuting the notion that perch behaviour was a form of parental care. In contrast to other species, e.g., common eiders, *Somateria mollissima* (Öst & Tierala, 2011), we did not find that perch behaviour increased for mothers when vulnerable young were present. In species where mothers show maternal care, such as ungulates, mothers provide extra vigilance so that their offspring can increase their time spent feeding (Pays et al., 2012), which could explain our finding that juveniles do not spend a similar amount of time perched as adults. Instead, juveniles spent more time foraging than adults or subadults. To summarise, perch behaviour in the Barbary ground squirrels may be more affected by environmental conditions than social conditions.

Our results also suggest that perch behaviour did not impose survival costs or benefits in that: 1) distance to cover was shorter for perched individuals than foragers, and, 2) there was no relation between the proportions of time spent perched on survival, Julian date lived until, and age at disappearance. However, we were unable to measure predation risk for perched individuals compared to foragers directly 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 behaviour alone as in groups. This result suggests there is a selfish benefit to the perched individual, such as increased detection of predators (Bednekoff, 2001; Bednekoff & Woolfenden, 2003). Another possibility for the absence of an effect on survival is that all individuals in the population perform perch behaviour with juveniles performing the least amount, but juvenile mortality rate is higher than (sub)adult mortality rate (Chapter 2). In summary, we found no apparent cost or benefit of perch behaviour in the Barbary ground squirrel.

Concluding Remarks and Future Studies

Our results suggest that perch behaviour was synchronised in this invasive population of Barbary ground squirrels. Furthermore, kin selection was not a mechanism explaining coordinated vigilance in this species with varying relatedness levels within groups. Two non-mutually exclusive hypotheses explaining synchronisation of perch bouts in the Barbary ground squirrels are that: 1) the squirrels are satiated and have the time and energy to perform synchronised perch behaviour (cost is low), and, 2) the benefits are large in terms of evading terrestrial predators that are ambush predators. Future studies could test for other possible hypotheses explaining synchrony of perch bouts, including contagion-of-fear, induced synchrony, and mimicking of nearest neighbour hypotheses (Sirot and Touzalin 2009, Beauchamp 2015), since the group members must be monitoring each other's vigilance level. This study adds to the growing literature of synchronised vigilance, explores the function of synchronised and collective behaviour, and shows that the cost of the trade-off between vigilance and foraging may not be high for an invasive species.

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Table 6.1 Hypotheses and predictions on perch behaviour in Barbary ground squirrels on Fuerteventura, Canary Islands, Spain

	Hypothesis	Predictions
Perch behaviour	Perch = induced vigilance	0) Individuals only perch in the presence of an external stimulus, e.g., predator
	Perch = sentinel behaviour	1) perched from elevated positions 2) continuous turn-over without changing the number of perched individuals any more than expected by chance
	Perch = synchronised behaviour	3) either multiple individuals are perched or non-vigilant at the same time
Perch behaviour and social conditions	Social conditions influences who are perched	4) adults and sub-adults spent more time perched than juveniles 5) individuals only perch when close kin are nearby (kin-selected behaviour) 6) adult females only perch when their own vulnerable offspring have emerged (parental behaviour)
Perch behaviour and survival	Survival increases for perched individuals	7) perched individuals are closer to cover than individuals performing another behaviour & individuals are perched when alone and in a group
	Survival decreases for perched individuals	8) greater risk of predation when located at raised positions & when in worse body condition

Perch behaviour is defined as vigilance without performing any other behaviour for over 30 s

and at raised positions of at least 10 cm above the ground.

Table 6.2 The proportion of observed and expected time without perched individuals (denoted as mean \pm SE) for observation period in Barbary ground squirrels calculated as duration of perch bouts

Observation period	<i>n</i>	observed	expected	$P_{\text{obs}}-P_{\text{exp}}$	<i>V</i>	<i>P</i>
All individuals	125	0.19 \pm 0.02	0.54 \pm 0.03	-0.36 \pm 0.03	496	<0.001
Adults	122	0.20 \pm 0.02	0.52 \pm 0.03	-0.33 \pm 0.03	158	<0.001
Adult females	107	0.19 \pm 0.02	0.52 \pm 0.03	-0.35 \pm 0.02	20	<0.001

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

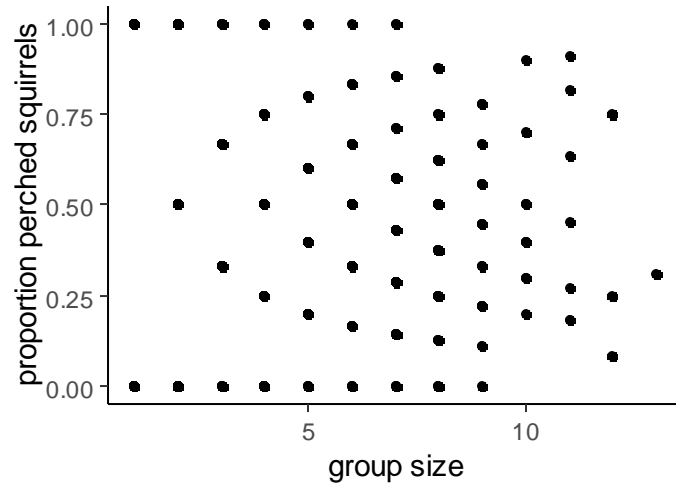


Figure 6.1 The absence of a relationship between the proportion of perched group members and group size in Barbary ground squirrels on Fuerteventura, Spain (beta regression: $y = -0.33 + 0.02x$; LR test: $\lambda = 0.55$, $P = 0.46$).

Chapter 7 Overall discussion

The five data chapters of this thesis addressed the life history (Chapter 2), social organisation (Chapter 3), and some of the selection pressures influencing group living in the Barbary ground squirrel (Chapters 4, 5 and 6). Barbary ground squirrels show a 'fast' life-history and thus show potential for rapid population growth, which may have contributed together with habitat characteristics and other species characteristics to their invasion success (Chapter 2). My results suggest that social patterns in female Barbary ground squirrels arise due to female philopatry and that unrelated males group through male-biased dispersal (Chapter 3). This species shows sexual segregation of sleeping burrows, but both males and females can be seen foraging, being vigilant, moving around, and affiliatively and/or agonistically interacting in the same area throughout the day. As they show spatiotemporal overlap and affiliative behaviours, we can consider them social, supporting our hypothesis that diurnal rodents living in arid environments can be social. Next, I questioned whether the Barbary ground squirrels are social to avoid predation. They show partial collective detection of predators because as group size increased, individual low- and high-quality vigilance did not decrease, but collective high-quality vigilance increased (Chapter 4), and they use alarm calls to warn group members of danger (Chapter 4 and 5). The absence of a group-size effect for individual high-quality vigilance can be explained since the Barbary ground squirrels synchronise their high-quality vigilance/"perch" bouts (Chapter 6). The constraints of living as a diurnal species in an arid environment, habitat structure, and predation pressure are possible selective pressures selecting for grouping in the Barbary ground squirrel.

Population growth in Barbary ground squirrels is influenced by a fast life history. As rainfall can influence population dynamics of arid-adapted species (Previtali, Lima, Meserve,

Kelt, & Gutierrez, 2009) due to the resource pulse following a rainfall event (Shenbrot, 2014), favourable environmental conditions could have influenced Barbary ground squirrel population growth as well. Some possible patterns were observable with only three years of field work: My first field season was very dry and was also a year after a long period of little rainfall, some subadults were present in the population and litter size was on average two. Whereas the last two years received more precipitation, no subadults were present, average litter size was three, and some females had a second litter within the same year. These findings suggest that population growth was exponential in years with more precipitation and that the generation time was halved in years with favourable environmental conditions. Similar patterns were found in tree squirrels, where reproductive output can be doubled in years with good rainfall and consequently greater food availability (Cudworth & Koprowski, 2013; Gurnell, 1983). Furthermore, shorter generation times in the introduction phase, especially, could have helped the Barbary ground squirrel population to grow rapidly and to become established on Fuerteventura. Yet, three field seasons is not a sufficient period to identify patterns in life history and sociality strategies or population dynamics (Hayes & Schradin, 2017), therefore long-term data could show patterns of how this species could adapt to changing environments.

Barbary ground squirrels are active year-round and males and females live in groups, which are segregated during the night but share space throughout the day, suggesting a form of fission-fusion dynamics (Aureli et al., 2008; Sueur et al., 2011). These social patterns do not fit the indices of sociality of the temperate ground-dwelling sciurids, which is categorised in the following levels from low to high: solitary/asocial, single-family female kin clusters, female kin clusters/male territoriality, polygynous harems/male dominance, and egalitarian polygynous harems (Armitage, 1981; Michener, 1983). Additionally, Blumstein and Armitage (1998) found

that in temperate ground-dwelling sciurids, species with reproductive skew, later maturity, smaller litters, and higher juvenile survival showed greater social complexity. Barbary ground squirrels show no reproductive skew in years with favourable conditions as all adult females breed, have early maturity, and large litters, therefore they should not be socially complex. However, fission-fusion dynamics may introduce a different level of social complexity.

Barbary ground squirrels fission into primarily same-sex sleeping burrow associations throughout the night, but can fuse with the other sleeping associations during the day. All individuals within the site can then be considered the community with the sleeping burrow associations as the subunits. These dynamics also explain the different social group definitions I have used throughout my thesis, as I defined a social group as individuals sharing a sleeping burrow together (Chapter 3), or as individuals present within 60 m of one another (van der Marel, López-Darias, & Waterman, 2019). A similar, but opposite pattern of fission-fusion is seen in hamadryas baboons, *Papio hamadryas*, where individuals fusion into larger groups at night to reduce predation risk, but come morning they separate into smaller foraging groups (Kummer, 1971). Fission-fusion dynamics in giraffes, *Giraffa camelopardalis* sp., has been hypothesised to have evolved in order for the giraffes to efficiently forage for unpredictable and dispersed food resources by using long-distance vocalisations to share information with kin, while group fusion is used to maintain the kin bonds (Bercovitch & Berry, 2013). For Barbary ground squirrels, the observed pattern may have evolved to reduce predation risk and to exploit clustered resources.

Female social groups in Barbary ground squirrels had an average coefficient of relatedness of 0.26 and were predicted to not show high levels of organisational or relational complexity (Lukas & Clutton-Brock, 2018). Relational complexity occurs in societies where

relatedness among group members is low and where the relationships among group members (e.g., dominance hierarchy) define an individual's social status within the group (Lukas & Clutton-Brock, 2018). However, Lukas & Clutton-Brock (2018) only present insight into the social complexity of female groups, suggesting that combining male and female sociality might introduce a different level of social complexity similar to species living in groups with fission-fusion dynamics (Aureli et al., 2008; Sueur et al., 2011). Conversely, organisational complexity, measured by the number of demographic roles in a group, often occurs in societies where relatedness among group members is high and where a division between breeders and non-breeders is present. In this type of societies, non-breeders are reproductively suppressed and provide alloparental care to the offspring of breeders (Lukas & Clutton-Brock, 2018). Therefore, species with cooperative breeding and alloparental care are suggested to be more complex, because adults tolerating young other than their own is suggested to be an essential step for social complexity (Lott, 1984; Rayor & Armitage, 1991). Cooperative breeding is suggested to occur only in species with high relatedness among group members (Lukas & Clutton-Brock, 2018). However, cooperative breeding can also be present in species with lower levels of relatedness due to promiscuity and low levels of reproductive skew (Kramer & Russell, 2014), as in the Cape ground squirrel, *Xerus inauris* (Pettitt & Waterman, 2011; Waterman, 1995; Waterman & Archibald, 2018). It is possible that female Barbary ground squirrels are facultative communal or cooperative breeders, with some females staying solitary, while other females share their sleeping burrow with up to four other females raising their litter together (Chapter 3). Thus, the social patterns of Barbary ground squirrels may be more complex than predicted for the relational and organisational complexity hypotheses (Lukas & Clutton-Brock, 2018).

Species or groups with greater social complexity are also hypothesised to have a more complex communication system ('social complexity hypothesis', Freeberg et al., 2012), which is supported in different taxa (e.g., parid species, Krams, Krama, Freeberg, Kullberg, & Lucas, 2012; and ground-dwelling sciurids, Pollard & Blumstein, 2012). For example, ground-dwelling sciurids with different demographic roles have a greater vocal repertoire and social group size in these species explains the ability to discriminate individual calls (Blumstein, 2007; Pollard & Blumstein, 2011). Chapters 4 and 5 provide the first description of the alarm call repertoire of Barbary ground squirrels. They have two distinct alarm call types, but social group size is on average three individuals in both female and male social groups, and subadults do not necessarily have to be present (Chapter 3). The small amount of different demographic roles within a social group could explain the absence of variation in alarm call repertoire size. However, as discussed previously, Barbary ground squirrels do not fit the sociality indices of temperate ground-dwelling sciurids (Armitage, 1981; Blumstein & Armitage, 1998; Michener, 1983). Additionally, one alarm call (the 'whistle') was not recorded and therefore no objective measurement of alarm call repertoire size could be performed. Comparable to quantifying social complexity, acoustic communicative complexity has been measured mainly using the subjective measure of looking at spectrograms to categorise calls, but more objective methods, such as discriminant analysis, are available (Fischer, Wadewitz, & Hammerschmidt, 2017; Peckre, Kappeler, & Fichtel, 2019). Thus, even though there are not many demographic roles, which implies a low level of social complexity, the presence of both male and female social groups does imply some level of social complexity. Therefore, I argue that the number of demographic roles or group size is not sufficient to characterise the social complexity of this species. Besides, the number of different alarm calls may not correctly characterise communicative complexity, as Barbary ground

squirrels may use other signals, such as olfactory (e.g., scent marking) or visual signals (e.g., tail-flagging). If the squirrels use multimodal signalling, they are more complex in their communication system. In the social complexity hypothesis often only one signal has been studied, therefore investigating this hypothesis offers a promising future research avenue (Peckre et al., 2019).

My results show that the Barbary ground squirrel is another species in the tribe Xerini that is social, besides the highly social Cape ground squirrel (Waterman, 1995; Waterman & Archibald, 2018). However, the other ground squirrel species in this tribe living in semi-arid to arid environments are not social (Happold, 2013). The striped ground squirrel, *Xerus erythropus*, has been reported to live solitary or in pairs, and are not colonial or territorial (Herron & Waterman, 2004). Both the unstriped ground squirrel, *Xerus rutilus*, and the mountain ground squirrel, *Xerus princeps*, live solitary or in small family groups of the mother with her offspring, and no social interactions (e.g., allogrooming) occurred among the squirrels (Herzig-Straschil & Herzig, 1989; O'Shea, 1976). Thus, living in an arid environment to avoid predation is not the only selective pressure influencing sociality in diurnal prey species.

The openness of the habitat is another example of a constraint on sociality. Visual cues are essential for predator detection in diurnal species and thus for ground-dwelling sciurids, whereby predator detection is easier in a habitat with an open structure (Ylönen & Brown, 2007). The risk imposed in a given habitat (in terms of avoiding predation) can increase as the density of predators increases or when habitat structure (e.g., plant cover) interferes with predator detection (Ebensperger, 2001; Hoogland, 1981; Shuai et al., 2019). Furthermore, a higher level of sociality is predicted in species living in a riskier habitat compared to species living in safer habitats (Ebensperger, 2001). For the Barbary ground squirrel, habitat openness may influence

their vigilance as their high-quality vigilance or ‘perch’ bouts were synchronised, possibly functioning to watch for predators on both sides of the rock walls and dams that are present on Fuerteventura (Chapter 6). As such, vigilance could instead of being synchronised function as a form of group sentinel behaviour, meaning that multiple individuals (approximately 50% of the group, Chapter 6) have to be on the lookout to watch at either side of the rock walls. Whether high-quality vigilance in the Barbary ground squirrel works as a mechanism to watch each other’s back, i.e., watch for predators at either side of rock walls and dams, can be examined by observing the gaze, head, or body direction of the squirrels, as at least two squirrels have to be vigilant and watch in opposite directions of the rock walls.

Phylogenetic selective pressures are other constraints on sociality. These pressures are factors that species share through common ancestry (Rowe & Honeycutt, 2002). By mapping behavioural traits onto a phylogeny, historical patterns of social evolution can be detected. This type of comparative analysis allows one to determine if different species share social behaviour through common ancestry or through convergent evolution (Fuentes-González & Martins, 2019). For example, phylogenetic frameworks on eusociality in bees have provided insights in the origins of eusociality and the ancestral state that gave rise to eusociality (Danforth, Cardinal, Praz, Almeida, & Michez, 2013). A phylogenetic meta-analysis of habitat and activity patterns on body and group size in primates showed that diurnal primate species have larger social group sizes (Fuentes-González & Martins, 2019), supporting the hypothesis that group living is favoured to reduce predation risk in diurnal species (Randall, 2007; Shultz, Opie, & Atkinson, 2011). In the primate genus *Eulemur*, social organisation is influenced by phylogeny in comparison to environmental factors (Ossi & Kamilar, 2006). In carnivores, cooperative hunting and predator avoidance are two proposed selective pressures explaining grouping (Schneider &

Kappeler, 2014). In hystricognath rodents, both phylogeny and vegetation cover explain the presence or absence of grouping (Sobrero, Inostroza-Michael, Hernández, & Ebensperger, 2014). These comparative studies permit us to decouple drivers of sociality, including habitat characteristics and phylogeny, in the African ground squirrels, in ground-dwelling sciurids, or in other animal species.

Even though my study provides data on the social organisation of Barbary ground squirrels (Chapter 3), I did not define their level of sociality. Conventionally, the measures of social complexity often differ per studied taxa making comparisons difficult. For example, in primates, three levels of social organisation are characterised (Schaik & Hooff, 1983), whereas in temperate ground-dwelling sciurids, social organisation is categorised into five different levels (Armitage, 1981; Michener, 1983). Therefore, there has been no consensus on how to define social complexity (Kappeler, Clutton-Brock, Shultz, & Lukas, 2019) as it was quantified by group size (Ebensperger & Blumstein, 2006), the number of demographic roles in a group (Blumstein & Armitage, 1998), the number of differentiated relationships among conspecifics (Bergman & Beehner, 2015) across varying contexts (Freeberg et al., 2012), by the distribution of differentiated relationships within a group (Fischer, Farnworth, Sennhenn-Reulen, & Hammerschmidt, 2017), or by quantifying associations using mixture models (Weiss, Franks, Croft, & Whitehead, 2019). In that a quantitative measure over a qualitative measure of social complexity is preferred (Avilés & Harwood, 2012), four components of the social system – social organisation, social structure, mating system, and care system – have been suggested as quantitative measures of social complexity thus facilitating comparisons among different taxa or among populations of the same species (Kappeler, 2019). Therefore, future research could focus

on the other three components, besides the social organisation, to compare Barbary ground squirrels to either closely related species or other species living in similar environments.

To understand social evolution in all its details, an integrative approach involving Tinbergen's four questions should be adopted with an emphasis on variation in social systems, proximate mechanisms, and evolutionary change (Robinson, Grozinger, & Whitfield, 2005). A step forward to an integrative approach has been made in social insects (Kapheim, 2018). But with the current advances in technology (Ghoul, Andersen, & West, 2017; Rittschof & Robinson, 2014; Robinson et al., 2005; Rubenstein & Hofmann, 2015), an integrative approach could be extended to other taxa, other than social insects (Kapheim, 2018), that show variation in social complexity to fully comprehend the development, mechanism, function, and evolution of sociality (Hofmann et al., 2014).

This thesis not only advances our understanding of sociality but also provides valuable insight into population growth and corresponding invasion success of an introduced species. Invasive species provide a unique framework to study evolution over a relatively short timeframe (Allendorf & Lundquist, 2003). Barbary ground squirrels were introduced to Fuerteventura 53 years ago and with a generation time of approximately one year (occasionally half a year, Chapter 2), they provide an excellent model system in which to study the evolution of sociality and population biology, particularly, as we know so much about the details of their introduction, i.e., the exact number of founders and the location of their source population. Additionally, intraspecific variation in sociality is not well-studied (Kappeler et al., 2019; but see Maher, 2006; Schradin, 2013; Schradin & Pillay, 2005). As I focused on an invasive population of Barbary ground squirrels with different selective pressures influencing their sociality, e.g., different predator species, varying levels of predation pressure and parasite load, my results on the social

organisation and behaviour of this population may be different compared to the population in the endemic range. Therefore, further studies could focus on the social system of the population in the endemic region, preferably in the area where the first two founding individuals were from (López-Darias & Lobo, 2008; Machado, 1979). One could test whether the invasive population evolved new behaviours or adapted different strategies compared to the endemic population.

To truly understand why the Barbary ground squirrel has so successfully invaded the island of Fuerteventura, we need data on their life histories and social system in both their introduced and native range and only by understanding their basic biology will we be in the position to control and minimise the ecological damage this species causes in their new habitat. Finally, my thesis addresses the knowledge gap that exists in the sociality literature on the selective pressures that influence grouping in African ground squirrels, which will aid in our understanding of the evolution of sociality in general.

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Appendices

Table A1. Life history traits recorded for invasive mammalian species adopted from Capellini, Baker, Allen, Street, & Venditti (2015, licensed under [CC BY](#)).

Binomial	NoLocs	LG	BM	GT	WA	NBM	LS	LY	AFB	RLy
<i>Ammotragus_lervia</i>	19	21.7	94202.2	156.2	121.7	4500.0	1.2	2.0	407.6	20.6
<i>Antilope_cervicapra</i>	9	23.9	36301.1	166.6	59.5	3386.1	1.2	2.0	669.2	22.1
<i>Atlantoxerus_getulus</i>	1	9.0	221.1	43.5	66.0	8.1	2.9	1.0	344.8	4.1
<i>Axis_axis</i>	47	20.8	69500.0	227.5	121.7	3156.9	1.0	1.0	450.0	19.6
<i>Bubalus_bubalis</i>	19	34.9	929501.0	320.0	240.3	37500.0	1.5	1.0	605.1	33.2
<i>Camelus_bactrianus</i>	21	40.0	554515.9	398.0	368.1	34346.6	1.4	1.0	1460.0	36.0
<i>Capra_hircus</i>	290	20.8	47386.5	156.0	158.0	2136.1	1.5	1.0	669.2	19.0
<i>Castor_canadensis</i>	17	23.4	18124.4	111.6	46.5	415.2	3.6	1.0	657.4	21.6
<i>Cervus_elaphus</i>	51	31.5	240867.1	235.6	104.6	8255.8	1.1	0.9	993.7	28.8
<i>Cervus_nippon</i>	86	26.3	53000.0	223.7	197.7	4277.1	1.0	1.0	1095.0	23.3
<i>Dama_dama</i>	73	25.0	57224.6	230.0	177.6	4698.4	1.0	1.0	1095.0	22.0
<i>Didelphis_marsupialis</i>	6	4.2	1134.8	14.0	92.5	0.2	7.1	2.0	182.5	3.7
<i>Equus_caballus</i>	21	62.0	403598.5	339.0	341.8	37900.0	1.0	1.0	912.5	59.5
<i>Erinaceus_europaeus</i>	35	14.0	778.0	37.0	40.0	15.5	4.6	1.5	349.8	13.0
<i>Genetta_genetta</i>	5	34.0	1756.2	74.2	71.8	77.8	2.3	2.0	1480.4	29.9
<i>Hemitragus_jemlahicus</i>	4	21.8	68616.4	195.8	151.3	2700.0	1.0	1.0	730.0	19.8
<i>Lepus_europaeus</i>	50	12.0	3816.4	42.0	30.4	123.0	2.1	4.4	236.5	11.4
<i>Macropus_rufogriseus</i>	13	19.0	16850.0	30.0	426.2	0.5	1.0	1.0	501.9	17.6
<i>Muntiacus_reevesi</i>	8	23.2	13499.9	214.2	60.0	1050.0	1.0	1.5	182.6	22.7
<i>Mus_musculus</i>	220	6.0	19.3	19.6	21.5	1.1	5.5	4.5	139.5	5.6
<i>Mustela_erminea</i>	9	12.5	284.5	66.4	60.9	2.3	6.7	1.0	95.0	12.2
<i>Mustela_nivalis</i>	14	10.0	78.5	36.5	36.7	2.0	5.1	1.0	113.5	9.7
<i>Mustela_putorius</i>	22	14.0	975.6	41.5	54.4	9.5	8.5	1.0	304.4	13.2

<i>Myocastor_coypus</i>	50	12.0	6361.6	131.9	52.8	205.7	5.3	2.6	319.4	11.1
<i>Myodes_glareolus</i>	1	4.9	20.7	19.7	19.7	1.8	4.3	3.5	83.2	4.7
<i>Neovison_vison</i>	93	11.4	925.0	42.0	56.0	8.5	4.5	1.0	261.3	10.7
<i>Nyctereutes_procyonoides</i>	47	16.6	4215.0	61.8	49.7	87.4	6.4	1.0	730.0	14.6
<i>Odocoileus_hemionus</i>	18	22.0	84560.6	203.5	73.5	3007.5	1.6	1.0	547.5	20.5
<i>Odocoileus_virginianus</i>	22	23.0	75901.3	201.4	79.9	2950.0	1.6	1.0	463.0	21.7
<i>Ondatra_zibethicus</i>	350	10.0	991.3	27.9	27.8	22.0	6.6	2.4	365.0	9.0
<i>Oryctolagus_cuniculus</i>	860	18.0	1590.6	30.5	26.3	39.1	5.2	4.5	121.7	17.7
<i>Petaurus_breviceps</i>	1	17.8	120.8	16.7	118.7	0.2	1.8	1.3	403.0	16.7
<i>Procyon_lotor</i>	43	21.0	6373.7	65.0	104.2	82.5	3.1	1.0	345.2	20.1
<i>Rattus_exulans</i>	120	1.1	50.6	21.3	28.0	2.4	3.7	3.9	173.6	0.6
<i>Rattus_norvegicus</i>	80	3.8	282.9	21.7	25.4	5.8	9.0	3.5	91.3	3.6
<i>Rattus_rattus</i>	130	4.2	142.7	23.5	28.0	4.5	5.9	3.8	143.1	3.8
<i>Rupicapra_rupicapra</i>	4	22.0	33266.4	178.3	76.0	2250.0	1.0	0.9	1368.8	18.3
<i>Rusa_timorensis</i>	32	20.0	66375.5	250.3	227.5	2532.0	1.0	1.0	630.0	18.3
<i>Rusa_unicolor</i>	9	26.4	177522.9	246.0	70.0	10270.0	1.0	1.0	788.4	24.2
<i>Sciurus_carolinensis</i>	50	24.0	545.4	44.8	69.5	15.2	3.0	2.0	365.0	23.0
<i>Sciurus_vulgaris</i>	9	14.8	333.0	38.0	64.5	8.8	4.5	2.0	273.8	14.1
<i>Sorex_minutus</i>	1	2.0	4.3	23.8	23.5	0.2	6.0	1.5	289.0	1.2
<i>Suncus_murinus</i>	26	3.2	43.8	30.2	19.2	2.4	3.1	9.8	46.9	3.1
<i>Sus_scrofa</i>	240	27.0	84471.5	115.2	97.9	807.8	4.5	1.5	312.0	26.1
<i>Sylvilagus_floridanus</i>	10	9.8	1207.2	27.0	22.8	34.2	4.6	4.8	123.6	9.5
<i>Tamias_sibiricus</i>	11	9.6	94.2	35.0	29.7	3.8	5.0	1.0	350.0	8.6
<i>Trichosurus_vulpecula</i>	36	15.9	2685.4	17.5	191.6	0.2	1.0	1.5	547.5	14.4
<i>Vulpes_vulpes</i>	23	21.3	4820.4	52.5	50.7	100.5	4.6	0.9	297.1	20.5

NoLocs = introduction effort, LG = longevity in years, BM = body mass in grams, GT = gestation time in days, WA = weaning age in days, NBM = neonatal body mass in days, LS = litter size, LY = litters per year, AFB = age at first birth in days, Rly = reproductive lifespan.

Table A2. Life history characteristics and number of founders for squirrel species that were successfully introduced, that successfully established, and that successfully spread (adopted from Bertolino, 2009)

Binomial	Stage ¹	NoLocs	Founders	LG	BM	GT	WA	LS	LY	AFB	RL
<i>Atlantoxerus_getulus</i>	Spread	1	2	9	220	43.5	66	2.9	1	305.1	1522.155
<i>Callosciurus_erythreus</i>	Est	28	10	17	366.1	48	45	2	2	365	5840
<i>Callosciurus_erythreus</i>	Spread	28	50	17	366.1	48	45	2	2	365	5840
<i>Callosciurus_erythreus</i>	Spread	28	100	17	366.1	48	45	2	2	365	5840
<i>Callosciurus_erythreus</i>	Spread	28	9	17	366.1	48	45	2	2	365	5840
<i>Callosciurus_erythreus</i>	Spread	28	5	17	366.1	48	45	2	2	365	5840
<i>Callosciurus_erythreus</i>	Spread	28	10	17	366.1	48	45	2	2	365	5840
<i>Callosciurus_erythreus</i>	Spread	28	10	17	366.1	48	45	2	2	365	5840
<i>Callosciurus_erythreus</i>	Est	28	15	17	366.1	48	45	2	2	365	5840
<i>Callosciurus_erythreus</i>	Spread	28	15	17	366.1	48	45	2	2	365	5840
<i>Callosciurus_erythreus</i>	Spread	28	4	17	366.1	48	45	2	2	365	5840
<i>Callosciurus_erythreus</i>	Est	28	2	17	366.1	48	45	2	2	365	5840
<i>Callosciurus_finlaysonii</i>	Est	3	4	12.8	278	NA	NA	1.5	3	730	3942
<i>Callosciurus_finlaysonii</i>	Est	3	7	12.8	278	NA	NA	1.5	3	730	3942
<i>Funambulus_pennantii</i>	Est	2	5	7	102.49	41.77	56	2.95	2.5	233.7546	2321.245
<i>Funambulus_pennantii</i>	Intro	2	5	7	102.49	41.77	56	2.95	2.5	233.7546	2321.245
<i>Sciurus_aberti</i>	Spread	14	4	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aberti</i>	Spread	14	100	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aberti</i>	Spread	14	91	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aberti</i>	Spread	14	42	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aberti</i>	Spread	14	8	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aberti</i>	Spread	14	4	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aberti</i>	Spread	14	59	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aberti</i>	Spread	14	111	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aberti</i>	Spread	14	43	7	620	43	70	3.5	1	327	2228

<i>Sciurus_aberti</i>	Spread	14	69	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aberti</i>	Spread	14	21	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aberti</i>	Spread	14	16	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aberti</i>	Spread	14	13	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aberti</i>	Intro	14	12	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aberti</i>	Intro	14	2	7	620	43	70	3.5	1	327	2228
<i>Sciurus_aureogaster</i>	Spread	2	4	11.5	455.57	NA	NA	1.94	NA	NA	NA
<i>Sciurus_carolinensis</i>	Spread	50	4	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Intro	50	3	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	10	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	3	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	100	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	5	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	25	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	91	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	36	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	4	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	5	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	8	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	2	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	5	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	14	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	4	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	2	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	6	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Est	50	8	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Intro	50	2	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	12	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	20	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	30	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	12	24	545.4	44.79	69.47	2.98	2	365	8395

<i>Sciurus_carolinensis</i>	Spread	50	12	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Intro	50	10	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	7	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	3	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	4	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	5	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Intro	50	10	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	6	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Spread	50	10	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Est	50	7	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Est	50	2	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_carolinensis</i>	Intro	50	2	24	545.4	44.79	69.47	2.98	2	365	8395
<i>Sciurus_niger</i>	Spread	7	12	16	803.7	45.35083	76.092	2.71	1.64	359.4586	5480.541
<i>Sciurus_niger</i>	Spread	7	50	16	803.7	45.35083	76.092	2.71	1.64	359.4586	5480.541
<i>Sciurus_niger</i>	Spread	7	5	16	803.7	45.35083	76.092	2.71	1.64	359.4586	5480.541
<i>Sciurus_niger</i>	Spread	7	4	16	803.7	45.35083	76.092	2.71	1.64	359.4586	5480.541
<i>Sciurus_niger</i>	Spread	7	18	16	803.7	45.35083	76.092	2.71	1.64	359.4586	5480.541
<i>Sciurus_niger</i>	Est	7	44	16	803.7	45.35083	76.092	2.71	1.64	359.4586	5480.541
<i>Sciurus_vulgaris</i>	Est	9	10	14.8	333	38	64.51	4.5	2	273.75	5128.25
<i>Sciurus_vulgaris</i>	Est	9	4	14.8	333	38	64.51	4.5	2	273.75	5128.25
<i>Sciurus_vulgaris</i>	Spread	9	30	14.8	333	38	64.51	4.5	2	273.75	5128.25
<i>Tamias_sibiricus</i>	Est	11	10	9.6	94.16	34.98	29.69	5.01	1	350.0232	3153.977
<i>Tamias_sibiricus</i>	Spread	11	85	9.6	94.16	34.98	29.69	5.01	1	350.0232	3153.977
<i>Tamias_sibiricus</i>	Spread	11	10	9.6	94.16	34.98	29.69	5.01	1	350.0232	3153.977
<i>Tamias_sibiricus</i>	Spread	11	10	9.6	94.16	34.98	29.69	5.01	1	350.0232	3153.977
<i>Tamias_sibiricus</i>	Spread	11	17	9.6	94.16	34.98	29.69	5.01	1	350.0232	3153.977
<i>Tamias_sibiricus</i>	Est	11	30	9.6	94.16	34.98	29.69	5.01	1	350.0232	3153.977
<i>Tamias_sibiricus</i>	Intro	11	400	9.6	94.16	34.98	29.69	5.01	1	350.0232	3153.977
<i>Tamias_sibiricus</i>	Intro	11	3	9.6	94.16	34.98	29.69	5.01	1	350.0232	3153.977
<i>Tamias_striatus</i>	Est	2	2	9.5	95.7	31.3499	35.61106	4.22	1.53	152.184	3315.316
<i>Tamias_townsendii</i>	Spread	2	36	9.3	79.12	28	41.76	3.75	1	353.6756	3040.824

¹ Stage refers to the status of the species: Intro = introduced, Est = established, and Spread = spread/invasive. NoLocs = introduction effort, Founders = number of individuals introduced, LG = longevity in years, BM = body mass in grams, GT = gestation time in days, WA = weaning age in days, NBM = neonatal body mass in grams, LS = litter size, LY = litters per year, AFB = age at first birth in days, Rly = reproductive lifespan.

Table A3 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 A4. Ethogram of recorded behaviours in the Barbary ground squirrels (adopted from Waterman 1995)

Category	Behaviour	Description
Affiliative interactions	Allogroom	Bite fur or move paws over fur or tail to remove dirt/ectoparasites of another squirrel
	Approach	Move within 2 m of another individual
	Follow	Walking in pursuit of another individual for >1 m or into a burrow
	Greet	Squirrels come close with their heads together, but they do not touch
	Kiss	Touch noses with another individual
	Move away	Squirrel walks away from approaching individual
	Sniff another	Mutual contact with naso-oral areas
Agonistic interactions	Chase	Pursuit after another individual by loping or running locomotion
	Displace	Approach another individual (within 2 m) who then moves away. Focal squirrel moves to spot where the other squirrel just left
	Jump at or away	One squirrel leaps at or away from another squirrel
	Run at	Using running locomotion to approach another squirrel
Antipredator	High-quality vigilance	Looking around from a raised position (>30 cm above ground) for > 30 s
	Low-quality vigilance	Looking around while performing another behaviour, such as feeding, or when looking around lasts < 30 s or from positions < 30 cm above the ground
Clean	Alarm call	Vocalisation alerting group members
	Autogroom	Bite fur or move paws over fur or tail to remove dirt/ectoparasites
Foraging	Sandbathe	Rolling in the sand and/or throwing dust/sand with front paws over the body
	Foraging	Actively searching for, manipulating, and/or ingesting a food item
Locomotion	Walking	Forward locomotion on all fours by placing one paw in front of the other, two paws are planted at any given time
	Loping	Intermediate forward locomotion
	Running	Fast forward locomotion, paws can be lifted from the ground at once
	Climbing	Ascending or descending a rock wall, tree or other objects
Sit	Sit (S2)	Squirrel remained only with its back paws on the ground, front paws are held in front of ventrum, back is slightly arched forward
	Sit (S4)	Squirrel rests with all four feet on the ground

Table A5. Microsatellite characteristics of loci developed for Barbary ground squirrels (*A. getulus*) on Fuerteventura, Spain

Locus	Dye label ¹ Primer sequence	Repeat motif	T _A (°C)	N _A	Allele size	H _O	H _E
Aget1	^{PET} AAACCCTATCTTCCTTCTATGAGC	AGAT	55	8	160-175	0.21	0.74
Aget3	^{FAM} AAATACAAATCCACACACAAGAGG	AAAAG	55	2	168-178	0.21	0.60
Aget4	^{NED} GCTGTGCTCTCTTCATGATTCTC	ACAG	55	4	180-195	0.22	0.62
Aget8	^{PET} ACAGGAGCCCATTGTATATGTC	ATCC	55	4	230-240	0.36	0.67
Aget17	^{FAM} AGACATGATCACTTAATTCCTCC	AGAT	55	5	320-374	0.38	0.68
Aget19	^{VIC} ATTCCCTCCAAGATATCCATCCC	AAAG	55	9	310-332	0.35	0.67
Aget23	^{FAM} TGGAATGTTTGGCCATATGTGAG	AGAT	60	4	370-384	0.21	0.72
Aget34	^{FAM} GGGATGCTTTAATACTGAGTCCC	AGAT	55	3	473-485	0.27	0.68
Aget42	^{FAM} AAACCCTTCTTATCACATGCACC	AGAT	55	5	320-375	0.33	0.68
Xin09 ¹	^{FAM} CCTCATCACAACCAAGACAG	GT	55	4	160-170	0.17	0.58
Xin10 ¹	^{FAM} CAGATTGAGAGTGAGAGGTG	GT	55	6	212-235	0.24	0.62

Annealing temperature (T_A), number of alleles (N_A), and observed and expected heterozygosities (H_O/H_E) are provided.

¹Xin loci were developed for the closely related Cape ground squirrel (*Xerus inauris*; Manjerovic et al., 2009).

²The step-up thermocycle profile was 95°C for 5 minutes (1x), then a cycle of 94°C for 30s, the step-up (45°C 10 times 30s, 55°C 20 times for 30s, and 72°C for 30s (32x)), ending with 72°C for 30 min and an infinite hold at 8°C (1x).

Text A1. Characterisation of microsatellite loci in the invasive Barbary ground squirrel

We had a library of more than 300 potential unique primer pairs (300 loci for microsatellite genotyping) of the Barbary ground squirrels that were constructed by the Evolutionary Genetics Core Facility (EGCF) at Cornell University, Ithaca, NY, USA, in 2014. We amplified previously developed Cape ground squirrel primers and three of these worked for the Barbary ground squirrel (Xin09, Xin10, and Xin26, Manjerovic, Waterman, Hoffman, & Parkinson, 2009). We performed PCR reactions using 10 µl of 50 non-labeled potential universal primers using the thermocycler (Applied Biosystems SimpliAmp Thermal Cycler, Thermo Fisher Scientific, Waltham, MA, USA). The PCR reaction consisted of 5.20 µl nuclease-free water, 2.00 µl 5 x buffer (1x), 0.60 µl 1.5 mM MgCl₂, 0.20 µl 0.2 mM dNTP, 0.10 µl 20 µM Forward longtag primer, 0.10 µl 20 µM Reverse primer, 0.10 µl 0.5 U Gotaq, and 1.0 µl (10-150 ng/µL) DNA. The thermocycler profile was set at 95° C for 5 minutes (1x), then a cycle of 94° C for 30 s, the annealing temperature (48° C, 50° C, 55° C or 60° C) for 30 s, and 72° C for 30 s (32x), ending with 72° C for 30 min and an infinite hold at 8° C (1x). We tested 5 µl PCR product of 50 potential non-labeled primers mixed with 2 µl 4 x BPB and loaded in wells of 1 % agarose gel stained with GelRed for 60 minutes at 115 Volts on three DNA samples and a negative. Loci that showed variation were tested on the capillary-based fluorescent gene sequencer ABI 3730XL (Applied Biosystems by Life Technologies, Carlsbad, CA, USA) at The Centre for Applied Genomics (TCAG, Sickkids, Toronto, ON, Canada). We direct labelled 11 loci on the 5'-end of the forward primer with the fluorescent dye FAM (IDTDNA, Coralville, IA, USA), 6 loci with PET, 3 loci with NED, and 2 loci with VIC (Life Technologies, Carlsbad, CA, USA). We performed PCR reactions of 20 µM labelled primers using the same recipe and thermocycler as before and sent the PCR products to TCAG. We assessed polymorphism of the markers using

Genemarker (SoftGenetics, LLC., State College, PA, USA). Genemarker scored the loci semi-automatically, after which the scored alleles were inspected by two different researchers, which is considered one of the most objective scoring procedures (Pompanon, Bonin, Bellemain, & Taberlet, 2005).

Table A6. Summary statistics of our observation periods per site on Fuerteventura

	\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).

Text A2. Spectral analysis of Barbary ground squirrel alarm calls

We randomised the alarm call files ($n = 17$) before quantifying the acoustic parameters to minimise order bias. For each vocalisation, we selected a section of 10 s with the highest signal-to-noise ratio to measure the call rate and average syllable duration. We selected the fourth syllable from the beginning of that section to quantify the spectral properties (following the protocol by J. Hare, personal communication, 24 February 2017): the maximum and minimum frequency; the frequency of maximum power (the frequency with the greatest energy, called peak frequency); the total bandwidth (the change in frequency from the maximum to minimum frequency at the start and end of the syllable). When primary syllables of the alarm calls were preceded by a brief element, we measured the latency to the primary syllable, the duration, the bandwidth and the frequency rate change, i.e., the total bandwidth of the preceding element divided by its duration (after Sloan et al. 2005). We considered this brief element, hereafter called a first element or ‘chip’, as an affix to the alarm call. We extracted all measures using the bioacoustics program Avisoft-SASlab Pro (Avisoft Bioacoustics, Glienicke, Germany). We performed high-pass filters at 1.3 kHz to minimize confounding noise for all vocalisations (Matrosova, Volodin, & Volodina, 2009). We generated the sound spectrograms of the alarm vocalisations using a Hamming-window, a Fast Fourier Transformation (FFT) length of 1024 with a 100% frame size, and 98.43% overlap (J. Hare, personal communication, 24 February 2017). Values are presented as the mean \pm SE in Appendix Table A7.

Table A7. Selected spectral parameters of the repeated alarm barks of Barbary ground squirrels recorded on Fuerteventura, Spain

Label	Call rate	Syllable duration		Frequency			Bandwidth	Chip			
		Mean	SE	Min	Max	Peak	Total	Latency	Duration	Bandwidth	Frequency rate change
2	1.83	0.17	0.01	1.46	12.57	4.45	11.11	0.04	0.04	9.26	228.08
3	1.62	0.14	0.10	1.93	8.09	3.07	6.16	0.03	0.03	1.25	42.66
4	2.20	0.14	0.02	1.89	8.31	2.98	6.42	0.04	0.02	1.81	84.58
5	1.60	0.19	0.02	1.29	10.29	4.56	9.00	0.03	0.04	10.00	276.24
11	1.84	0.16	0.01	1.80	7.83	4.41	6.28				
13	1.21	0.16	0.25	1.46	7.83	2.77	6.37				
15	1.48	0.12	0.02	2.84	7.23	3.15	4.39				
22	1.56	0.13	0.04	1.67	6.11	2.40	4.44				
23	1.20	0.16	0.07	1.55	9.81	2.96	8.26	0.01	0.01	1.38	97.87
24	1.94	0.11	0.02	2.32	5.68	2.60	3.36				
25	1.95	0.17	0.01	1.46	6.11	2.87	4.65				
26	1.73	0.12	0.02	1.67	6.63	2.90	4.96				
30	1.50	0.20	0.02	1.63	13.78	3.16	12.15	0.03	0.03	0.95	34.93
31	1.72	0.22	0.03	1.50	9.68	2.94	8.18	0.03	0.04	0.99	37.50
35	1.66	0.14	0.10	2.32	14.55	6.16	12.23				
39	1.32	0.14	0.03	2.58	7.49	2.94	4.91				
40	1.86	0.14	0.05	1.33	7.32	3.12	5.99				

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