

Vigilance and Collective Detection of Predators in Degus (*Octodon degus*)

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Abstract

Individuals of social and partially social species typically reduce their vigilance activity when foraging in groups. As a result, per capita risk of predation decreases and individuals allocate more time to foraging and other fitness rewarding activities. Reduction of per capita risk is hypothesized to occur because there are more individuals to detect potential predators. If so, collective (i.e. total) vigilance is expected to increase with foraging group size. Increased surveillance during group foraging may occur if group members scan independently of one another, or sequentially to avoid the overlapping of their vigilance bouts. Intriguingly, such coordinated vigilance assumes that individuals monitor not only the presence, but the vigilance behaviour of group mates. We used seasonal records on time budget and grouping patterns of individually marked degus (*Octodon degus*), a social rodent, to examine if (a) individual vigilance decreases and/or foraging increases with group size, (b) collective vigilance increases with group size and (c) foraging degus coordinate their vigilance. When foraging, degus decreased their individual vigilance and increased their foraging time when in larger groups. Despite this, degus in larger groups increased their collective vigilance, supporting the hypothesis that socially foraging degus decrease predation risk through an improved ability to detect and escape potential predators. Additionally, patterns of collective vigilance suggested that degus scan independently of each other and so, they do not coordinate their vigilance to prevent its temporal overlapping. This finding does not support that foraging degus monitor the vigilance activity of group mates.

Introduction

The observation that individuals of social and partially social species typically reduce their vigilance activity when foraging in groups is common (Elgar 1989). However, the hypothesized causes of this 'group-size effect' on vigilance vary (Roberts 1996; Beauchamp 2001, 2003; Barbosa 2002). One major hypothesis states that, as group size increases, per capita risk of predation decreases and individuals

allocate more time to foraging and other fitness rewarding activities (Elgar 1989; Quenette 1990; Roberts 1996). Reduction of per capita risk may occur because there are alternative prey (i.e. the dilution hypothesis; Foster & Treherne 1981) or because there are more individuals to detect potential predators (i.e. the detection or 'many eyes' hypothesis; Pulliam 1973). In both cases, the group-size effect reflects a net benefit derived from variations in predation risk (Blumstein et al. 2001).

Although dilution and detection effects are likely to interact in affecting an individual's risk of predation (Bednekoff & Lima 1998a), the degree to which dilution and detection are influencing the evolution of anti-predator vigilance is difficult to examine, mostly because both benefits predict individual scanning should decrease with increasing group size (Childress & Lung 2003). Nevertheless, if individuals in a group benefit primarily by detection rather than dilution, collective (i.e. total) vigilance is expected to increase with group size, a prediction supported in a bird (Bertram 1980) and some mammals (Jarman 1987; Childress & Lung 2003) where collective vigilance has been measured directly (but not in others: Quenette & Gerard 1992; Fernández et al. 2003). As a consequence, individuals in groups improve their ability to detect and escape potential predators (Lima 1995a), a prediction supported in some birds (Powell 1974; Siegfried & Underhill 1975; Kenward 1978; Lazarus 1979; Møller 1987; Boland 2003) and a few small mammals (Hoogland 1981; Ebensperger & Wallem 2002). This prediction assumes, in turn, that foragers share information perfectly and instantly when they detect predators. Although such an assumption may seem unrealistic in some cases (Lima 1995b), individual foragers may gather information from predator detection quickly, particularly so in species where individuals give alarm calls.

Increased surveillance during group foraging may result if group members scan independently of one another (Pulliam 1973; Bednekoff & Lima 1998b), a frequently untested assumption in studies assessing collective vigilance (Barnard 1980; Monaghan & Metcalfe 1985; Yáber & Herrera 1994; Vásquez 1997). However, increased group vigilance also may result if individuals within groups scan sequentially to avoid overlapping vigilance bouts (e.g. McGowan & Woolfenden 1989). Such coordinated vigilance assumes that individuals monitor not only the presence, but the vigilance behaviour of group mates (Pulliam et al. 1982; Lima 1995a), a debated issue (e.g. Bednekoff & Lima 1998b). On the one hand, some recent experimental evidence supports that starlings (*Sturnus vulgaris*) monitor group mates' vigilance during social foraging (Fernández-Juricic et al. 2004, 2005). In contrast, other studies failed to support visual monitoring of vigilance in three other species of birds (Lima 1995a; Beauchamp 2002; Fernández et al. 2003). From a theoretical point of view, the monitoring of group mates' vigilance would be unlikely given the relatively low benefits expected compared with the costs (Ward 1985; Bednekoff & Lima 1998a; but see Ferriere et al. 1996).

Therefore, additional empirical evidence assessing whether foragers alter their vigilance in response to the vigilance of group mates is needed.

We collected seasonal records on time budget and grouping patterns of degus (*Octodon degus*), a caviomorph rodent, to examine how collective vigilance varies with group size. Degus are small- to medium-sized (approx. 180 g), diurnal and social rodents of the semiarid and seasonal environments of north-central Chile (Fulk 1976; Yáñez 1976; Le Boulengé & Fuentes 1978). In these habitats, degus construct underground burrows and galleries that are used communally (Ebensperger et al. 2004). When above ground, degus forage (mostly on grasses and forbs) solitarily or in small groups (mean = 2 individuals, range = 1–10; Ebensperger & Hurtado 2005a, this study). A previous study recorded degus to decrease their individual vigilance with group size (i.e. the typical group-size effect on vigilance) and predicted collective vigilance to increase with group size (Vásquez 1997). The observation that group-foraging degus detect the approach of a simulated predator at a greater distance than solitary foraging degus is consistent with this prediction (Ebensperger & Wallem 2002). Both anecdotal and systematic data support degus use predator-specific alarm calls to warn conspecifics against aerial and terrestrial predators (Fulk 1976; Yáñez 1976; Cecchi et al. 2003), suggesting degus foragers share information when they detect these predators. Taken together, these lines of evidence suggest predation risk is a major influence on degu behaviour and that these rodents are an adequate subject to examine the extent of cooperative vigilance during foraging.

In short, we examined whether (i) individual vigilance decreases with group size, leaving more time available to foraging, (ii) collective vigilance increases with group size and (iii) whether socially foraging degus cooperate through synchronizing their vigilance, implying they monitor the behaviour of group mates.

Materials and Methods

Study Area and Time of Observations

The study population is located at the Estación Experimental Rinconada de Maipú, (33°23'S; 70°31'W, altitude = 495 m), a field station of the Universidad de Chile located 30 km west of Santiago, Chile. The study site is characterized by a Mediterranean climate, with warm, dry summers and cold, wet winters. The site consists of a flat area

dominated by scattered shrubs (*Proustia pungens*, *Acacia caven* and *Baccharis* spp.) and containing grasses and forbs. Shrub cover, as assessed from nine 200 m linear transects, is low and reaches $14.5 \pm 3.5\%$ ($\bar{x} \pm SE$). Animals were monitored in an area of 1.13 ha, chosen for study based on evidence of degu activity, including the presence of recently used burrow entrances and direct visual sightings of animals.

Observations were carried out seasonally (i.e. once every 3 mo) and as part of a more general field study conducted between June 2002 and January 2004. Every year, we spent 10–15 d in Jun. (early Austral winter), Oct. (mid Austral spring), Jan. (mid Austral summer) and Apr. (mid Austral autumn). Overall, two winter, two summer, two spring and one autumn seasons were monitored (but see below). This sampling schedule follows major events of degus' life cycle. Degus are seasonal breeders: in our study site, degus typically mate in late autumn (May to Jun.), with parturitions in late winter to early spring (Sep. to Oct.; Ebersperger & Hurtado 2005a).

Capture and Marking of Degus

Members of the study population were captured using Sherman live traps (H.B. Sherman Traps Inc., Tallahassee, FL, USA) baited with rolled oats. As degus are strictly diurnal (Kenagy et al. 2002; Ebersperger et al. 2004), traps were placed near active burrow entrances during morning and evening hours, when the animals were most active above ground. Traps were checked approximately every hour; captured animals were removed from traps as soon as they were encountered. We sexed and marked all adults captured (i.e. above 120 g) with neck collars (made of plastic cable ties wrapped in coloured tape) to allow visual identification during behavioural observations (see below). We used a colour key where two to three of seven different tape colours (including black and white) were combined in a single animal. Typically, trapping was conducted for 5–7 d per season. Trapping effort per season ranged between 1100 and 1540 trap-days.

Behavioural Observations

We observed degus above a portable tower-blind at a distance of 30–80 m, depending on the location and height of surrounding vegetation. Observer height (ground to eye level) was 4.3 m. Animals were identified on the basis of collar colour; identification was facilitated by the use of a 10 × 50 pair of

binoculars. As soon as a collared degu was sighted, we recorded its behaviour with a Sony digital video camera (model DCR-TRV330, Sony Corporation, Japan). Video recordings were terminated after approx. 40 min or when the focal subject went out of sight for more than 3 min. The length of focal observations averaged 11 (± 8) min and ranged from 1 to 41 min. In the lab, one of us (MJH) played back the videos and recorded the percentage of time that individual degus spent in different activities when above ground.

Degus were considered to be vigilant when they remained motionless with their heads raised and either supported by four legs (quadruped) or on rear legs (bipedal) (Vásquez 1997). Foraging degus adopted a crouching posture with the head lowered to ground level (Vásquez 1997). On average, vigilance and foraging accounts for $78 \pm 2\%$ of degus' time budget (Ebersperger & Hurtado 2005a). Therefore, we included focal observations of degus only if foraging and vigilance activity accounted for at least 70% of estimated activity budget. This criterion made our observations comparable with previous studies (e.g. Vásquez 1997). Other elements of behaviour were recorded and reported elsewhere (Ebersperger & Hurtado 2005a). We quantified the number of degus located near each focal animal from video recordings. To do so, we included all degus being at a distance of 2–3 m from our focal individual. We used this criterion because (i) it ensures that all putative members of foraging groups are in visual contact of each other, a condition needed to detect group-size effects on vigilance (Blumstein 1996) and (ii) because previous studies have recorded that this distance significantly influences vigilance activity of degus (Vásquez 1997; Ebersperger & Wallem 2002; Vásquez et al. 2002). Degus leave or join the groups freely and continuously during social foraging. Thus, when the size of the foraging group that included the focal animal changed during our focal observations (because an animal either moved in or left the group), we distinguished activity performed by the focal animal under different group size categories. Ongoing observations at our study site revealed that 14% ($n = 51$) of all focally recorded degus were animals from five different and well-identified social groups (Ebersperger et al. 2004); the remaining focal degus were of unknown social units.

Collective vigilance was assessed directly rather than estimated. Following others (Bertram 1980; Fernández et al. 2003), we recorded collective vigilance as the proportion of time that at least one individual of the group was vigilant.

To control for some potentially confounding variables (Elgar 1989), we restricted our behavioural records to adult sized individuals that were active in similarly open, exposed habitat, monitored density of open burrows (i.e. refuges), distinguished male from females and did not include data from spring season when pups and young individuals were present (i.e. two seasons were discarded). All these variables, including age-differences, habitat openness, sex-differences and the presence of young individuals influence vigilance and foraging activity of ground-dwelling rodents (Holmes 1984; Loughry 1993; Yáber & Herrera 1994; Armitage et al. 1996). We confirmed that density of open burrows did not vary during the realization of this study (Ebensperger & Hurtado 2005b). Observations were completed between 07:30 and 12:00 hours during warm seasons and between 09:30 and 15:00 hours during cold seasons, which matches the animals' daily activity above ground through seasons (Kenagy et al. 2002). Observations were carried out on days with similar weather conditions and we avoided conditions that might affect our ability to detect degus (i.e. no observations were conducted on days with dense fog, heavy winds, or rain). To homogenize any potential effect of trapping on degu behaviour, observations always took place 3 d after trapping ended.

Data Independence and Analysis

All focal observations were carried out on individually marked degus. Scan sampling data carried out simultaneously (Ebensperger & Hurtado 2005a) revealed that the mean number of degus that were present in our study area ranged from 14 (± 1 individuals, summer 2004) to 44 (± 1 individuals, Summer 2003). Of these, the number of degus that were individually marked (or remarked) before any behavioural sampling period ranged from 15 to 43 animals (28 ± 2 animals).

For each degu observed at each group size (1–10 individuals), we calculated the mean proportion of time allocated to individual vigilance. To avoid pseudoreplication, focal degus contributed with a single behavioural record to any given group size category (Fernández et al. 2003). However, two sources of data dependency persisted. First, some individuals contributed to more than one group size category within seasons, an acceptable limitation given that temporal composition of degu foraging groups changes rapidly. Secondly, data across seasons were partially dependent because 12 of 51 (24% of all focal) individuals were recorded in two different seasons;

one more subject was recorded in three of five seasons sampled; no degus were recorded in more than three seasons. Nevertheless, our data pooling was limited and unlikely to have biased our overall analysis (Leger & Didrichsons 1994). Inter-individual differences in vigilance of solitary recorded degus were smaller than intra-individual differences (one-way ANOVA on individual vigilance, $F_{12,14} = 0.88$, $p = 0.581$).

To analyse the effect of group size on individual and collective vigilance we used multi-way analysis of covariance (Blumstein et al. 1999, 2001; Fernández et al. 2003). Thus we examined the proportion of time in sight allocated to vigilance and to the proportion of time that at least one individual of the group was vigilant (i.e. dependent variables). Seasonality was entered as a discrete random factor with five levels (one per season) and sex was entered as a discrete (two levels) fixed factor. We examined the influence of group size as a covariate instead of as a categorical variable because not all factor-level combinations (i.e. season x , sex y , group size z) were represented in the data set. Data on proportions of time spent in foraging and vigilance, and proportion of time at least one degu was vigilant were arcsine squared-root transformed to fit the assumptions of normal distribution (Kolmogorov–Smirnov test, $p > 0.20$) and homogeneity of variances (Levene's test, $p > 0.20$). Data on group size were $\text{Log}_{10}(x + 1)$ -transformed (Zar 1996).

We examined the possibility that degus monitor the vigilance of group mates by means of comparing patterns of observed collective vigilance with that expected from random and sequential bouts (Fernández et al. 2003). For each group size n , we took values for individual vigilance (V_i) from a normal distribution with parameters (mean and standard deviation, after arcsine of squared-root data transformation) equal to the observed values at each group size. As we obtained only one record for group of sizes of 7, 8 and 10 individuals, we pooled these data into a group size of 6 or more during this analysis. Expected random collective vigilance (V_c^r) was calculated by:

$$V_c^r = 1 - \prod_{i=1}^n (1 - V_i)$$

and expected sequential collective vigilance through:

$$V_c^s = \sum_{i=1}^n V_i$$

where n is the number of individual of the group and the values of V_c^s were constrained to a maximum

of 1. We ran 2000 simulations for each group size and the mean values were used as an estimate of collective vigilance, to be compared with the observed data.

Statistical analyses were performed using STATISTICA 6.0 (StatSoft Inc., Tulsa, OK, USA). We tested the fit of observed values of collective vigilance to those expected under the random and sequential models with the use of Bonferroni corrected one-sample Student's t-tests. All statistical tests were two-tailed. We followed Nakagawa & Foster (2004) in reporting the size of statistical effects and p-values, instead of reporting post hoc (retrospective) power analysis. Data are presented as $\bar{x} \pm SE$.

Results

Individual Vigilance and Foraging

The data set consisted of a total of 132 focal observations recorded on 47 degus (26 females and 21 males). Neither seasonality ($F_{4,121} = 0.91$, $p = 0.538$) nor sex of focal degu ($F_{1,121} = 4.46$, $p = 0.100$) influenced this aspect of degu vigilance significantly. In contrast, group size did influence degu vigilance negatively ($\beta = -0.213 \pm 0.085$) and significantly so ($F_{1,121} = 6.21$, $p = 0.014$), meaning that degus decreased their individual vigilance when in larger groups (Fig. 1a).

In the case of time allocated to foraging by degus, neither seasonality ($F_{4,121} = 0.53$, $p = 0.722$) nor sex ($F_{1,121} = 4.40$, $p = 0.101$) of focal degus influenced foraging time again. Similarly, group size did influence degu foraging directly ($\beta = 0.189 \pm 0.087$) and significantly so ($F_{1,121} = 4.74$, $p = 0.031$), meaning that degus increased their foraging when in larger groups (Fig. 1b).

Collective Vigilance

When collective vigilance was examined, neither seasonality ($F_{4,121} = 0.93$, $p = 0.528$) nor sex of focal degu ($F_{1,121} = 5.93$, $p = 0.070$) influenced collective vigilance significantly. As expected, group size did influence degu vigilance positively ($\beta = 0.305 \pm 0.081$) and significantly ($F_{1,121} = 14.01$, $p < 0.001$), meaning that degus experienced increased levels of collective vigilance when in larger groups (Fig. 1c).

Collective vigilance in groups of three, five and six (or more) degus did not differ from random expectations (Bonferroni corrected $p > 0.005$). In contrast, collective vigilance of degus when foraging in pairs

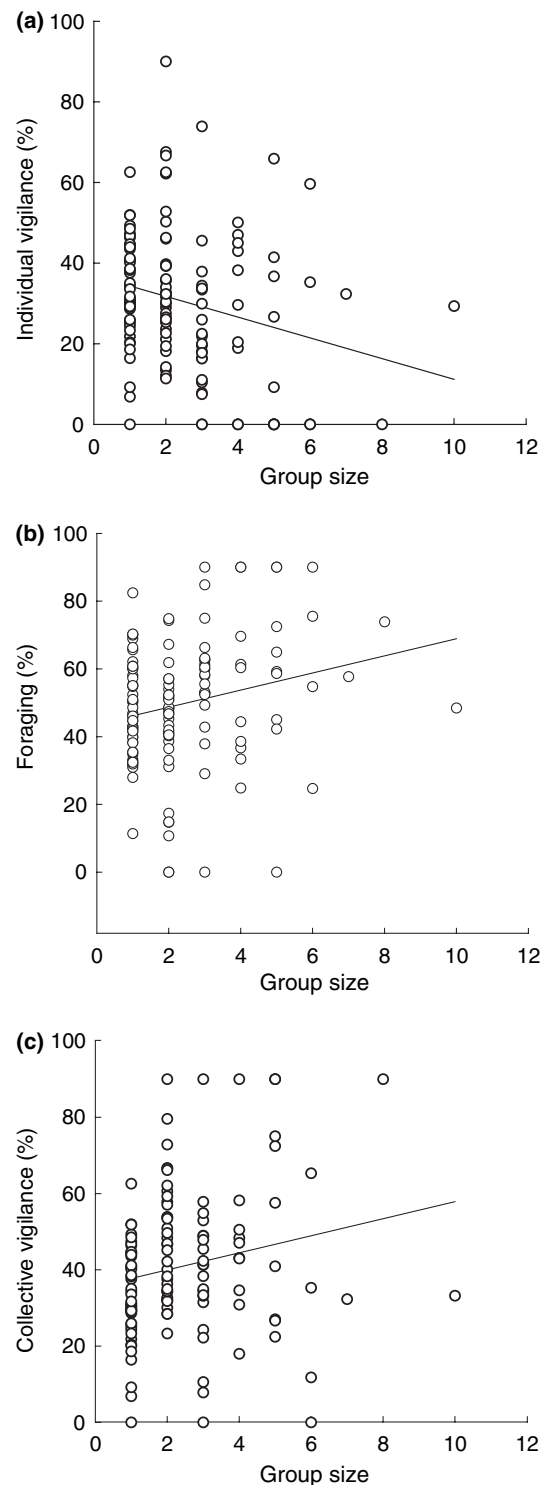


Fig. 1: Time (arcsine squared-root transformed %) allocated to individual vigilance (a) and foraging (b) in degus alone and in groups of up to 10 individuals; (c) time that at least one degu of the group was vigilant (i.e. collective vigilance, open circles). The data set consisted of a total of 132 focal observations recorded to 47 degus

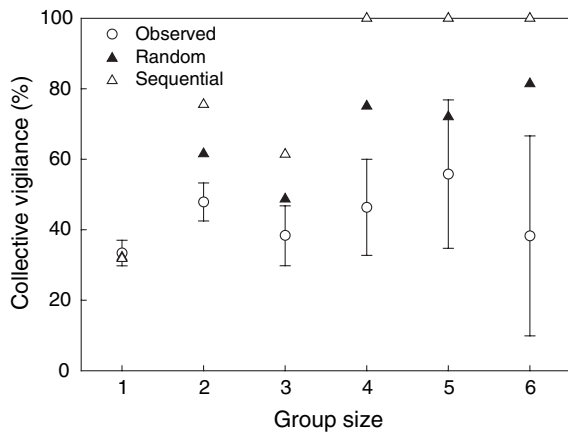


Fig. 2: Observed (open circles), randomly expected (filled triangles) and sequentially expected (open triangles) mean values of collective vigilance in degus (% time that at least one degu of the group was vigilant). Error bars represent $\pm 95\%$ confidence intervals

and in groups of four individuals was lower than expected from random ($p < 0.001$; Fig. 2). Collective vigilance of degus in groups was always lower than that expected from the sequential model ($p = 0.002$ or lower; Fig. 2).

Discussion

Individuals of socially foraging species typically reduce their vigilance activity when foraging in groups (Elgar 1989) and one major explanation of this 'group-size effect' on vigilance states that per capita risk of predation decreases in larger groups; as a consequence, individuals allocate more time to foraging and other fitness rewarding activities (Elgar 1989; Quenette 1990; Roberts 1996). Reduction of per capita risk may occur because there are alternative prey (i.e. the dilution hypothesis; Foster & Treherne 1981) or because there are more individuals to detect potential predators (i.e. the detection hypothesis; Pulliam 1973). Although dilution and detection effects are difficult to tease apart (Childress & Lung 2003), the detection effect clearly predicts collective vigilance should increase with group size. Our study supported this expectation. When foraging in groups (mostly of two to five individuals), degus decreased individual vigilance, increased their foraging activity and modestly enhanced collective vigilance, findings that confirmed previous suggestions (Vásquez 1997). Increased group vigilance may benefit group foraging degus through enhancing their ability to detect approaching predators, a possibility supported by the observation that degus detect and escape simulated predators at a larger distance

when in larger groups (Ebensperger & Wallem 2002). That individuals in groups improve their ability to detect and escape potential predators assumes foragers share information perfectly and instantly when they detect predators, an assumption that seems unrealistic (Lima 1995b). However, that foragers may share information instantly may be more realistic in species where individuals give alarm calls such as degus (Fulk 1976; Yáñez 1976; Cecchi et al. 2003). Currently, we lack most basic information about degu calls, but calls in other ground-dwelling and social rodents elicit quick (i.e. within a few seconds or less) anti-predator responses by non-callers such as heightened vigilance and running to nearby burrows (Blumstein 1998; Randall & Rogovin 2002).

Theoretically, increased collective surveillance during group foraging may result from individuals within groups scanning sequentially to avoid the overlapping of their vigilance bouts (e.g. McGowan & Woolfenden 1989). An intriguing consequence of such coordinated vigilance is that individuals monitor not only the presence, but the vigilance behaviour of group mates (Pulliam et al. 1982; Lima 1995a). Recent experimental evidence supports starlings (*S. vulgaris*) can monitor group mates' vigilance while foraging as they are capable of synchronizing their vigilance and target group mates when interrupting their foraging to scan (Fernández-Juricic et al. 2004, 2005). However, the social monitoring of vigilance has been questioned by other theoretical and empirical studies. Thus, Bednekoff & Lima (1998a) considered the monitoring of group mates' vigilance as highly unlikely given the relatively low theoretical benefits involved compared with the costs. This is particularly expected in the case of relatively large groups (Ward 1985). Regarding experimental evidence, no evidence of visual monitoring of vigilance was recorded in dark-eyed juncos (*Junco hyemalis*) where foraging individuals do not alter their vigilance in the presence of less vigilant group mates (Lima 1995a). Similarly, socially foraging zebra finches (*Taenopygia guttata*), subjected to partial obstructions that made social monitoring of group mates more difficult, did not change their own behaviour (Beauchamp 2002). Observational studies also have provided negative evidence: patterns of collective vigilance revealed either randomness or no synchronization in greater rheas (*Rhea americana*; Fernández et al. 2003), house sparrows (*Passer domesticus*; Elcavage & Caraco 1983), ostriches (*Struthio camelus*; Bertram 1980) and wild boars (*Sus scrofa*; Quenette & Gerard 1992). Patterns of collective

vigilance measured to degus adds to most previous evidence in that individuals scan independently of each other (i.e. randomly) and do not coordinate their vigilance to avoid time overlapping. However, the prevalence of random scanning still causes collective vigilance to be enhanced in some socially foraging species. Most importantly, enhanced collective vigilance increases predator detection in doves (*Streptopelia senegalensis*; Siegfried & Underhill 1975), emus (*Dromaius novaehollandiae*; Boland 2003), starlings (*S. vulgaris*, Powell 1974), red-billed weavers (*Quelea quelea*; Lazarus 1979), swallows (*Hirundo rustica*; Møller 1987), wood pigeons (*Columba palumbus*; Kenward 1978), degus (Ebensperger & Wallem 2002) and prairie dogs (*Cynomys* spp.; Hoogland 1981). Thus, collective detection of predators in most socially foraging species seems an emergent property of groups.

Collective vigilance of degus when foraging in pairs or in groups of four animals was lower than expected from individuals scanning at random (Fig. 2), suggesting degus under these social conditions were scanning rather simultaneously. Fernández et al. (2003) suggested simultaneous vigilance may result if vigilance events are elicited by stimuli of common interest, a pertinent hypothesis in the case of degus. When active above ground, degus frequently alarm call at real aerial predators (Fulk 1976; Cecchi et al. 2003), but also at other medium sized birds that fly over at low altitude (i.e. lapwings, *Vanellus chilensis*; L. A. Ebensperger pers. obs.). Alarm calls at both stimuli cause most individuals around callers to scan simultaneously.

In short, our study adds to the large amount of evidence demonstrating the group-size effect on vigilance (see Elgar 1989 for a review), but also adds to the less common body of evidence demonstrating that directly measured collective vigilance increases with group size in some social foraging animals (Bertram 1980; Jarman 1987; Childress & Lung 2003). In addition, patterns of collective vigilance in degus suggest individuals scan independently of each other, an observation providing no evidence for the social monitoring of group mates' vigilance.

Acknowledgements

We are greatly indebted to the Universidad de Chile, particularly to José Daniel García, Field Station Administrator, for providing the facilities during field work. Gustavo Fernández helped to clarify some issues when estimated expected values of collective vigilance and two anonymous reviewers kindly

helped to improve a previous version of this paper. Funding was provided by a FONDECYT grant 1020861. During the writing of this article, LAE was supported by the Centro de Estudios Avanzados en Ecología & Biodiversidad (FONDAP 1501-001). All research conducted as part of this study conformed to national and institutional guidelines for research on live mammals (permits No. 893 and 1894 by the Servicio Agrícola y Ganadero).

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