

Relatedness does not predict vigilance in a population of the social rodent *Octodon degus*

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Received: 2 January 2012 / Revised: 13 June 2012 / Accepted: 29 June 2012 / Published online: 14 July 2012
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Abstract The possibility that social foragers adjust and coordinate their scanning activity when in the presence of close relatives to attain inclusive fitness benefits remains controversial and scarcely examined. To this aim, we first tested the null hypothesis of no association between foraging individuals of the diurnal rodent, *Octodon degus* and their pairwise relatedness (six microsatellite loci), under natural conditions. Secondly, we examined the influence of relatedness on scan effort (percent overlapping) and temporal distribution of scanning using linear regression. Finally, we evaluated whether temporal distributions of scanning were significantly lower (coordination) or higher (synchrony) than random expectations using bootstrapping. We found that pairwise relatedness between focal degus and their foraging partner did not influence the scan effort or the temporal distribution of scanning. These original, field-based findings imply that vigilance behavior in socially foraging degus is unlikely to be kin-selected and adds to results from previous lab studies in that kinship remains a poor predictor of social behavior in these animals. Overall, our study adds to others revealing that kin selection may not have had an impact on aspects of social behavior such as vigilance during social foraging.

Keywords Scanning · Cooperation · Social foraging · Coordination · Synchrony

Introduction

In some social species, individual vigilance decreases in groups (i.e., “group size effect”, Elgar 1989; Lima 1995; Fairbanks and Dobson 2007; Beauchamp 2008), however, overall scanning activity, or collective vigilance, may increase and enhance detection of potential predators (e.g., Pulliam 1973; Pulliam et al. 1982; Elgar 1989; Quenette 1990; Roberts 1996). This collective benefit has been well recorded in birds (e.g., Siegfried and Underhill 1975; Kenward 1978; Lazarus 1979; Bertram 1980; Møller 1987; Boland 2003) and mammals (Jarman 1987; Ebensperger and Wallem 2002; Childress and Lung 2003; Ebensperger et al. 2006a; Pays et al. 2007a, b; however, see Carter et al. 2009; Favreau et al. 2010). Moreover, collective vigilance is maximized whenever group members coordinate their scanning in non-overlapping bouts, avoiding raising the head (i.e., being vigilant) whenever another group member is already vigilant (i.e., cooperative or coordinated scanning) (Bednekoff and Woolfenden 2003; Fernández-Juricic et al. 2004a). Evidence for coordinated scanning is mostly restricted to species with sentinels (e.g., Florida scrub jays *Aphelocoma coerulescens*: McGowan and Woolfenden 1989; Bednekoff and Woolfenden 2003; Arabian babblers *Turdoides squamiceps*: Wright et al. 2001; meerkats *Suricata suricatta*: Clutton-Brock et al. 1999; vervet monkeys, *Cercopithecus aethiops*: Horrocks and Hunte 1986). In contrast, field and experimental studies on other birds (e.g., Fernández et al. 2003; Fernández-Juricic et al. 2004b) and mammals (e.g., Pays et al. 2007b; Ebensperger et al. 2006a) failed to demonstrate coordination of vigilance.

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A requirement of coordinated scanning is that individuals monitor not only the presence but also the scanning activity of group mates (Lima 1995; Beauchamp 2002). However, monitoring group mates' scanning could be costly and prone to cheating (Ward 1985; Bednekoff and Lima 1998; Rodríguez-Gironés and Vásquez 2002), something that introduces a problem to reciprocity-based mechanisms (Dugatkin 1997). Thus, an alternative mechanism to cooperation through coordination of scanning activity may rely on kin selection, i.e., scanning coordination has been favored whenever individuals forage in the presence of close relatives.

An examination of the idea that coordinated scanning provides individuals with indirect benefits through kin selection (Hamilton 1964) remains controversial. We are aware of four field studies documenting how scan effort changes with relatedness within social groups, and these studies have provided mixed results. On the one hand, relatedness within social groups of Arabian babblers (Wright et al. 1999) and meerkats (Clutton-Brock et al. 1999) does not influence sentinel effort. Likewise, scan effort does not vary between Columbian ground squirrels (*Urocitellus columbianus*) with and without nearby kin (Fairbanks and Dobson 2010). In contrast, breeding Siberian jays (*Perisoreus infaustus*) spend more time vigilant while foraging with retained young (mature offspring that remain with the parents to help raise siblings) than in the presence of non-related flock members (Griesser 2003). Thus, evidence for scanning coordination is rare and restricted mostly to social species with sentinel behavior. Most studies aimed to examine how sentinel or scanning effort is influenced by relatedness failed to record an effect. However, the relation between coordination of scanning and relatedness has not been addressed directly. Herein, we examine this critical aspect of collective vigilance in a natural population of degus, a social and diurnally foraging rodent.

Degus (*Octodon degus*) are diurnal, small- to medium-sized rodents (Woods and Boraker 1975) that inhabit underground burrow systems in the semi-arid environment of central and northern Chile (Yáñez 1976; Meserve et al. 1984). When active above ground, degus forage solitarily or in small groups (mean=2 individuals, range=1–10), and foraging and vigilance take about 78 % of total activity time (Ebensperger and Hurtado 2005). A previous field study recorded degus to increase their collective vigilance when foraging socially but failed to record evidence of scan coordination (Ebensperger et al. 2006a). However, individual and collective levels of vigilance recorded were highly variable (Ebensperger et al. 2006a), implying that factors other than group size may explain some of this variation.

Whether genetic relatedness influences social behavior in degus remains unclear. On the one hand, degu social groups (i.e., the number of adults communally nesting; Hayes et al. 2009) include related and unrelated members (Ebensperger et al. 2004; Quirici et al. 2011a), and laboratory studies

support that degus use odor similarity to recognize and discriminate kin from non-kin (Jesseau et al. 2009; Villavicencio et al. 2009). Other lab studies, however, report no evidence that these rodents discriminate or adjust their behavior based on kinship (Ebensperger 2006b, Ebensperger et al. 2007), including vigilance (Quirici et al. 2008). However, these differences may be reconciled whenever the influence of kinship on social behavior of degus is context-dependent. For instance, it could be that monitoring group mates' scanning by captive subjects is scarcely beneficial compared with free-living subjects exposed to predator attacks.

In this study, we examined how relatedness influences degu behavior under natural conditions. Given that kin association is required for kin selection to operate (Hamilton 1964; Chesser 1991), we first tested the null hypothesis of no association between foraging degus and their pairwise relatedness using molecular markers. Secondly, we examined the influence of relatedness on scan effort (percent overlapping) and temporal distribution of scanning using linear regression. Finally, we evaluated whether temporal distribution of scanning was significantly lower (coordination) or higher (synchrony) than random expectations using bootstrapping approaches. Overall, we predicted that degus would be more likely to coordinate their scanning whenever they forage with other related as opposed to unrelated degus.

Materials and methods

Study site, trapping, and animal identity

Study was conducted during April–May (Austral Autumn) of 2008 at the Estación Experimental Rinconada de Maipú (33°23'S, 70°31'W, altitude 495 m), a field station of the Universidad de Chile. The study site is characterized by a Mediterranean climate with warm, dry summers (December–March) and cold wet winters (June–September) (Yáñez 1976; Meserve et al. 1984). The site consisted of open areas with scattered shrubs (*Proustia pungens*, *Accacia caven*, and *Baccharis* spp.) and annual grasses and forbs (Ebensperger and Hurtado 2005).

We trapped *O. degus* using a combination of Tomahawk (model 201, 14×14×40 cm, Tomahawk, Wisconsin, USA, 300 traps) and locally produced metal live-traps (30×10×9.5 cm, similar to Sherman traps, 300 traps), all baited with rolled oats. We set traps in burrow system entrances during 19 days from April 21 to May 11, at about 07:00 AM, prior to the emergence of adults. After 1.5 h, all traps were closed, and individual identity, sex, and body mass (grams) were recorded for every animal caught. Following similar field studies on social rodents (Verdolin 2007), adult aged degus (>6 months of age) were marked with unique stripe and dot combinations using Lady Clairol® black hair dye for

individual identification during subsequent behavioral observations. Upon first trapping, we removed a small piece of outer ear ($<15 \text{ mm}^2$) and stored these samples in 95 % ethanol for subsequent genetic analyses. We minimized pain of animals by making rapid cuts with sharp sterilized clipper. As required by our long-term demographic studies, degus were marked with metal tags on both ears (National Band & Tag Company Newport, KY, USA) (Quirici et al. 2011b). All procedures that involved handling of live animals were approved by the Pontificia Universidad Católica de Chile Bioethical Committee (DFCB-021-2008) and adhered to Chilean laws (permits 1-109/2008 [3542] by the Servicio Agrícola y Ganadero).

Behavioral data collection

We conducted our observations through 15–30 May (Austral Autumn). We observed degus from a hill side at a distance of 30–50 m depending on the location of the focal animal, from 10:00 to 17:00 h. This observation time matched the animals' main activity time at this time of year (Kenagy et al. 2002).

We restricted our observations to degus in pairs exclusively. We based this decision on that (1) scanning coordination is expected to benefit (i.e., be more likely) in smaller compared with larger foraging groups (Ward 1985; Rodríguez-Gironés and Vásquez 2002). (2) According to the spatial definition of foraging group size used in this and in previous studies (Vásquez 1997; Ebensperger and Wallem 2002; Vásquez et al. 2002), most (98 %) behavioral observations of social foraging involved subjects in pairs. Degus were considered to be in a foraging group whenever they remain within 2–3 m of one or more individuals. This inter-individual distance has been recorded to significantly influence vigilance and anti-predator behavior of degus (Vásquez 1997; Ebensperger and Wallem 2002; Vásquez et al. 2002). Finally, (3) we restricted our observations to degus in pairs to make these results comparable with a previous lab study (Quirici et al. 2008).

Soon after, two marked degus were sighted foraging (i.e., the animal typically assumes crouching posture with the head lowered to ground or directed toward the horizon); two of us (VQ and RS) recorded their behavior with a Sony digital video camera (model DCR-TRV330, Sony Corporation, Japan). Individual identification of every focal animal was aided with the use of 10×50 binoculars. Video recordings were terminated after 10 min or when the focal subject went out of sight. The length of focal observations averaged 10 ± 0.9 min and ranged from 8 to 11 min.

In the lab, one of us (MP) played back the videos and quantified time spent scanning (seconds) of focal and non-focal degus. We then calculated scan effort as the percentage of time that the focal degu spent scanning out of the time that both foraging degus were foraging socially (i.e., percent

overlapping). We haphazardly chose one degu of the pair as the focal animal.

An examination of the temporal distribution of scanning required us to record the activity of focal and non-focal subjects simultaneously, and we gathered such data from snapshots (Fernández-Juricic et al. 2004a, b). To make our results comparable with a previous study on social vigilance (Quirici et al. 2008), one of us (MP) recorded the behavior of focal and nonfocal subjects every 30 s. In particular, we considered degus to be vigilant whenever they remained motionless with their heads raised and either supported by four legs (quadruped) or on their rear legs (bipedal) (Vásquez 1997; Ebensperger et al. 2006a; Quirici et al. 2008). We recorded proportions of snapshots that focal and non-focal subjects were scanning.

To quantify the temporal distribution of scanning, we followed Quirici et al. (2008) and calculated a distribution scanning index $[DI=(Po-Pe)/Pe]$. We recorded individual frequencies of scanning by focal (π_i) and non-focal degus (π_j) and multiplied these values to compute the (expected) probability that both degus were scanning simultaneously under random expectations, Pe . Then, we calculated a distribution of scanning index (DI) considering Pe and the observed frequency of snapshots in which both animals were scanning, Po . Whenever this index approaches unity would imply degus are copying or scanning in synchrony. Values approaching -1 would indicate coordination.

Genetic methods

Details of DNA extraction and microsatellite procedures are reported in Quirici et al. (2011a). Briefly, DNA was extracted from tissue samples using the DNeasy Tissue Extraction Kit (QIAGEN, Inc.). Individuals were genotyped for four *Spalacopus cyanus* microsatellite loci (Scy1, Scy3, Scy5, and Scy6, Schroeder et al. 2000) and two degu microsatellite loci (OCDE1, OCDE3, Quan et al. 2009), under the conditions of Ebensperger et al. (2004) and Quan et al. (2009), respectively. These loci were polymorphic and showed no linkage disequilibrium in our study population.

Quantification of allele frequencies and analyses of linkage disequilibrium were conducted using GENEPOP 3.4 (Raymond and Rousset 1995). Deviations from Hardy–Weinberg equilibrium were evaluated using the Monte-Carlo randomization test of Guo and Thompson (1992) and the U-statistic of Rousset and Raymond (1995) as implemented in ML-Relate software (Kalinowski et al. 2006). Pairwise coefficient of relatedness (R) among individuals was calculated using the ML-Relate software (Kalinowski et al. 2006). The ML-Relate program was chosen because it provides maximum likelihood estimates of relatedness, a more robust approach compared with, for example, the

moment-based method (e.g., Queller and Goodnight 1989) (Milligan 2003). Calculations of R were performed adjusting relatedness to accommodate the possible presence of null alleles. We used R to refer to any estimate of genetic relatedness rather than r , which denotes the true relatedness based on knowledge of a pedigree (Winters and Waser 2003). R values close to 0.5 would be expected for first-order relatives (parents–offspring and full siblings); $R=0.25$ values would indicate second-order relatives (half siblings, grandsons, and nephews), $R=0.125$ values would indicate third-order relatives (cousins), and $R=0$ values would indicate unrelated individuals.

The number of alleles per locus and observed heterozygosity are reported in Quirici et al. (2011a). Briefly, the number of alleles per locus ranged from 2 to 10 (6.67 ± 2.66), and observed heterozygosity ranged from 0.26 to 0.77 (0.54 ± 0.17). Data from all six loci screened were included in our analyses of kinship.

Statistical analysis

Due to the possible effects of energy demands (e.g., Clutton-Brock et al. 1999; Wright et al. 1999) on degus vigilance, we first evaluated whether body mass influence time spent scanning (percent) and scanning index for the focal and non-focal individuals throughout linear regression.

We assessed correlations between behavioral association and R matrices with the Dietz's (1983) R -test and using 10,000 permutations, as implemented in SOCPROG 2.3 (Whitehead 2009). In our case, the behavioral association matrix is an estimate of number of times that one focal individual was foraging with another subject, divided by the total number of times this focal degu was recorded foraging. Numbers in this matrix ranged from 0 through 1, with 1 indicating that two degus were together every time each was sighted (Cairns and Schwager 1987; Ginsberg and Young 1992). A sampling period of 1 day was selected in SOCPROG to prevent behavioral observations were auto-correlated.

To examine the influence of relatedness on scan effort (percent overlapping) and temporal distribution of scanning (Distribution scanning index), we used linear regression considering pairs of females (female–female) and pairs that included males (male–male and male–female) separately. Due to the absence of correlation between pairwise relatedness and scan effort in pairs of females ($R^2=0.15$, $F_{1,11}=1.70$, $p=0.79$) or males ($R^2=0.05$, $F_{1,4}=0.17$, $p=0.29$), data were pooled together. Due to the absence of correlation between pairwise relatedness and DI in pairs of females ($R^2=0.12$, $F_{1,11}=1.40$, $p=0.74$) or males ($R^2=0.12$, $F_{1,4}=0.42$, $p=0.44$), data were pooled together. Data from degu pairs were considered as independent replicates, given that no dyads were registered twice.

Table 1 Individual ID, sex (M=males, F=females), body mass, and vigilance behavior and pairwise coefficient of relatedness of focal and non-focal degus used in the study

Focal	Body mass (g)	Non-focal	Body mass (g)	Total time together (s)	Focal: time spent scanning (%)	Non-focal: time spent scanning (%)	Scanning effort (% overlapping)	Distribution of scanning index (DI)	Pairwise coefficient of relatedness
F4254	136.3	F4151	176.4	244	9.4	4.9	16.1	−1.0	0.2
F3331	161.9	F0411	133.6	372	12.6	12.6	14.5	−1.0	0.0
F0215	139.7	F3331	161.9	191	2.6	6.8	5.2	−1.0	0.2
F1311	176.2	F0215	139.7	45	62.2	82.2	66.7	0.0	0.7
M1445	210.8	F3300	142.2	130	3.1	4.6	3.1	0.0	0.0
M0211	154.6	F0225	139.0	291	9.6	3.8	10.0	0.0	0.4
F1311	176.2	F0221	170.6	64	12.5	9.4	12.5	0.0	0.0
F3004	150.5	F1311	176.2	237	16.0	23.2	62.9	0.3	0.5
F4144	156.6	F3331	161.9	11	3.1	81.8	63.0	0.2	0.5
F0333	125.5	F3300	142.2	139	84.2	23.0	74.8	0.0	0.0
F0001	136.6	F4455	140.1	427	3.5	5.6	3.8	0.0	0.6
F4253	150.9	M1121	142.9	154	33.1	19.5	33.1	−0.0	0.1
M0005	177.3	F4151	176.4	90	5.6	6.7	4.4	0.3	0.0
F4455	140.1	M0005	177.3	50	70.0	54.0	70.0	0.2	0.0
F3300	142.2	F1130	174.8	150	23.4	24.2	31.5	0.3	0.0
F4423	152.0	F1130	174.8	136	20.1	20.1	16.1	−1.0	0.2
F0001	136.6	F4423	152.2	110	20.0	18.5	63.6	0.2	0.5
Mean	154.4		157.8	167.1	23.0	23.6	32.5	−0.2	0.2
SD	21.1		16.8	115.3	25.2	25.2	27.6	0.5	0.2

We evaluated whether DI values were significantly smaller (coordination) or larger (synchrony) than random expectations using bootstrapping. In particular, we calculated 10,000 values (with replacement) of DI from the 17 degu pairs. Then, we used the mean difference resampling (permutation) test to compare relatedness (R) between pairs of foraging degus whose observed DI values fell outside and to the left (i.e., indicating coordination) and to the right (i.e., synchrony) of 95 % confidence intervals. If relatedness influences temporal distribution of scanning, we were expecting high pairwise relatedness in degu foraging pairs whose negatives ID values fell outside the 95 % confidence interval. All statistical tests were two-tailed and conducted using the R 2.4.1 software (R Development Core Team 2006). Data are reported as means \pm SD. Differences were considered as statistically significant at $p < 0.05$.

Results

Behavioral observations

We found absence of correlation between focal degus body mass and time spent scanning ($R^2=0.13$, $F_{1,15}=2.24$, $p=0.15$) or scanning index ($R^2=0.11$, $F_{1,78}=1.78$, $p=0.20$). We found absence of correlation between non-focal degus body mass and time spent scanning ($R^2=0.03$, $F_{1,15}=0.49$, $p=0.49$) or scanning index ($R^2=0.07$, $F_{1,15}=1.22$, $p=0.28$). The same pattern was found when mean body mass (focal and non-focal) and time spent scanning ($R^2=0.02$, $F_{1,15}=0.31$, $p=0.59$) or scanning index ($R^2=0.19$, $F_{1,15}=3.75$, $p=0.07$) were analyzed.

Of the 43 marked degus, each subject contributed with one to three behavioral records (mean \pm SD=1.62 \pm 0.74). The duration of observations averaged 20 \pm 13 min (range, 10 to 60 min). This number of individually marked subjects rendered 17 focal observations in which both degus were visible and identified. These focal observations involved 22 different adult degus (18 females and 4 males) (Table 1). Mean time spent scanning (in percent), scan effort (percent overlapping), distribution scanning index (DI), and pairwise relatedness values are reported in Table 1. Six DI values fell outside 95 % IC [-0.75, 0.17], three of them representing negative values and three, positive values.

Relatedness and foraging associations

Pairwise relatedness between focal subjects and their foraging partners ranged from 0 to 0.73 (0.23 \pm 0.23 SD). Based on 10,000 permutations, we detected no correlation between genetic and behavioral associations (Dietz R -test, $R_D=-0.04$,

$p=0.79$). Thus, degus foraged with other individuals irrespective of their genetic similarity. Pairwise relatedness neither influenced variation in scan effort ($R^2=0.009$, $F_{1,15}=0.11$, $p=0.26$) (Fig. 1a) nor did variation linked to DI ($R^2=0.04$, $F_{1,15}=0.51$, $p=0.51$) (Fig. 1b). Pairwise relatedness between foraging pairs whose DI fell to the left of 95 % CI (i.e., implying vigilance coordination) was not different from pairwise relatedness between foraging pairs whose DI fell to the right of 95 % CI (i.e., implying vigilance synchrony) ($R_{\text{coordination}}=0.14\pm 0.12$ SD, $R_{\text{synchronization}}=0.33\pm 0.29$ SD, $p=0.41$).

Discussion

Collective vigilance is maximized whenever group members coordinate their scanning in non-overlapping bouts, avoiding raising the head whenever another group member is already vigilant (Bednekoff and Woolfenden 2003; Fernández-Juricic et al. 2004a, b). Given the costs of monitoring scanning behavior of the group mates (Ward 1985; Bednekoff and Lima

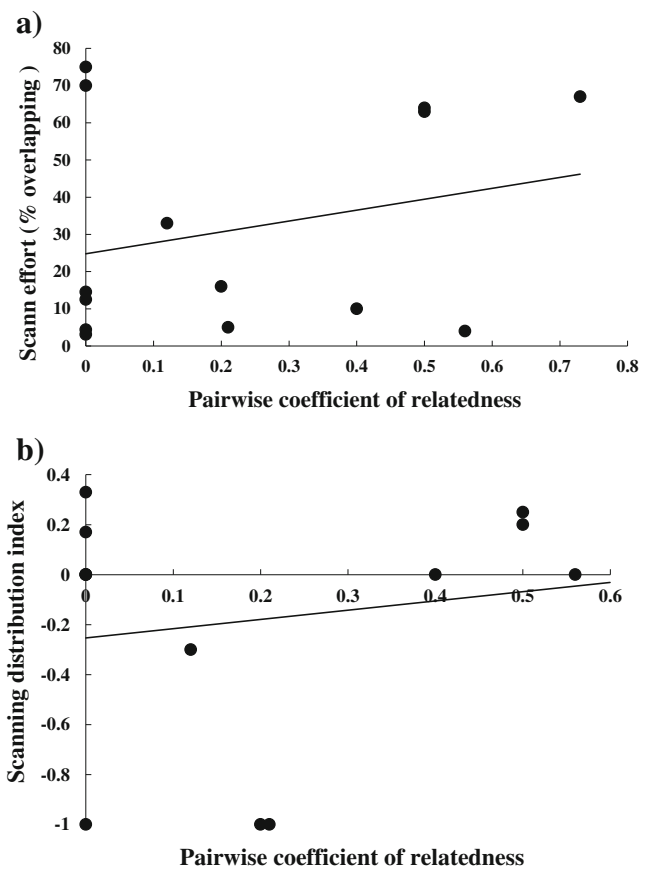


Fig. 1 Linear regression between pairwise coefficient of relatedness and a scan effort (percent overlapping) ($R^2=0.009$, $n=17$, $y=-10.37x+25.56$), and **b** distribution scanning index [DI=(Po–Pe)/Pe]: values approaches unity indicated synchrony, values approaching –1 indicate coordination, ($R^2=0.04$, $n=17$, $y=0.37x-0.25$)

1998; Rodríguez-Gironés and Vásquez 2002), individuals may derive additional indirect benefits whenever coordination of scanning is more likely among social foragers that are close relatives. We found that relatedness between socially foraging degus did not influence the temporal distribution of scanning. These results parallel the scanning behavior of these animals under controlled environmental conditions, i.e., pairs of foraging sisters were no more likely to coordinate their vigilance than completely unrelated foragers (Quirici et al. 2008). Taken together, available evidence indicates that vigilance behavior in degus has not been the target of kin selection. This conclusion should be considered with caution though. Firstly, our study is based on the behavior of 17 degu pairs recorded during one season of the year, and we cannot exclude the possibility that kin structure changes over seasons affecting the costs and benefits of scanning behavior in relation to relatedness. Changes in kin structure between years have been registered for example in the great tit (*Parus major*) (Dingemanse et al. 2004), the red grouse (*Lagopus lagopus*) (Piertney et al. 2008) and the banner-tailed kangaroo rat (*Dipodomys spectabilis*) (Busch et al. 2009). Given the small number of male subjects in our sample size, we cannot fully verify how gender may interact with relatedness to influence vigilance coordination.

Our results add to the small but slowly growing number of studies not supporting an effect of kinship on scanning activity by prey animals. Degus did not vary time spent scanning in response to varying relatedness between foragers, a result that parallels the scanning behavior of Columbian ground squirrels (Fairbanks and Dobson 2010). Moreover, sentinel effort in seemingly more complex forms of cooperation is explained by individual differences in physical condition or energy reserves instead of kinship (Clutton-Brock et al. 1999; Wright et al. 1999). We note, however, that an influence of physical condition on degu vigilance does not seem likely at this time. Neither time spent scanning nor scanning coordination was related to body mass differences.

Recent empirical and theoretical considerations suggest that kin selection may not be a major force driving social behavior of some organisms (Nowak et al. 2010). For instance, group foundation (i.e., sociality) and subsequent helping behavior may take place between genetically unrelated individuals (Queller et al. 2000), and direct competition among interacting relatives may outweigh its associated indirect benefits (West et al. 2001). Our study is the first to examine how the probability of vigilance coordination is influenced by kinship in a social species without sentinels. We found that vigilance is scarcely cooperative in socially foraging degus, and this relatively low level of cooperation is not influenced by kinship. These results further tilt the balance against kin selection as a force causing cooperative vigilance in prey animals.

Acknowledgments We are indebted to the Universidad de Chile, particularly to J. D. García (former) and to M. Orellana Reyes (current) Field Station Administrators, for providing the facilities during field work at Rinconada. V. Quirici was supported by Dirección de Investigación y Postgrado-Pontificia Universidad Católica de Chile (DIPUC), Program of Mejoramiento de la Calidad y la Equidad de la Educación Superior (MECESUP) and Program of Comisión Nacional Científica y Tecnológica (CONICYT) PhD fellowships. This study was funded by the grants Program of Comisión Nacional Científica y Tecnológica (CONICYT 2408003 to V. Q.); Fondo Nacional de Desarrollo Científico y Tecnológico (FONDECYT 1060499 to L. A. E.) and by the Center for the Advanced Studies in Ecology and Biodiversity (CASEB Program 1 and 7).

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