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Vigilance and social foraging in *Octodon degus* (Rodentia: Octodontidae) in central Chile

Vigilancia y forrajeo social en *Octodon degus* (Rodentia: Octodontidae) en Chile central

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ABSTRACT

Social foragers frequently show diminishing levels of per capita vigilance as the group size increases. This phenomenon, called the "group size effect", was studied in a natural population of the caviomorph rodent *Octodon degus*. Through field observations of groups of different size, I quantified the duration of bouts of vigilance and foraging. Results showed that degus spent significantly less time being vigilant as group size increased, which agrees with the group size effect. The reduction in vigilance was achieved through a decrease in the duration of vigilance bouts as well as in scanning rate. Further, foraging bouts of group members lasted longer with increasing group size. Total group vigilance also increased with group size. Degus adjusted their behavior in similar manner to that of other social feeding species. Time saved from vigilance was allocated to foraging. Group foraging may confer anti-predator as well as short-term feeding advantages to *O. degus*. Further studies in this area of research may help to understand the evolution of sociality in this species.

Key words: Anti-predator behavior, foraging, group size, *Octodon degus*, sociality.

RESUMEN

Con frecuencia, animales que forrajean socialmente muestran niveles menores de vigilancia individual a medida que crece el tamaño del grupo. Este fenómeno, llamado el "efecto de tamaño de grupo", fue estudiado en una población natural del roedor caviomorfo *Octodon degus*. Mediante observaciones de campo sobre grupos de distinto tamaño, cuantifiqué el tiempo que roedores focales invirtieron en eventos de vigilancia y forrajeo. Los *degus* asignaron significativamente menos tiempo en vigilancia cuando aumentó el tamaño del grupo, lo cual está en concordancia con las predicciones del efecto de tamaño de grupo. Esta reducción en vigilancia se alcanzó a través de una disminución en el tiempo de los eventos de vigilancia, así también como por una disminución en la tasa de eventos de vigilancia. Además, la duración de los eventos de forrajeo de los miembros de un grupo aumentaron con el tamaño de grupo. La vigilancia total del grupo también aumentó con el tamaño del grupo. Los *degus* ajustaron su comportamiento de modo similar al observado para otras especies que forrajean socialmente. El tiempo economizado por vigilancia fue asignado a forrajeo. El forrajeo en grupo puede conferir ventajas antidepredadoras, así también como ventajas de corto plazo en alimentación para *O. degus*. Estudios en esta área de investigación pueden ayudar a entender la evolución de la sociabilidad en esta especie.

Palabras clave: Conducta antidepredadora, forrajeo, *Octodon degus*, sociabilidad, tamaño de grupo.

INTRODUCTION

Increased protection from predators and enhanced resource acquisition are the most important presumed causes of social foraging (Clark & Mangel 1986). If all members of a social group are alerted once danger is detected, group members have the opportunity to be less vigilant while the overall group vigilance changes little. Consequently, individuals foraging in social groups spend less time in vigilance as a function of group size. This phenomenon, called the "group size effect" (e.g., Lima 1995a), represents the outcome of an underlying trade-off between vigilance and resource acquisition (see Elgar 1989, Lima & Dill 1990, Quenette 1990 for reviews). Any factor that relax the necessity of individual vigilance should lead to an increase in time to be allocated to food procurement and/or other related activities.

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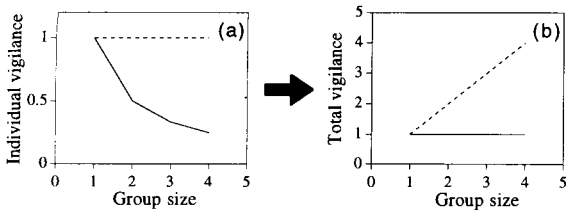

Fig. 1: The relationship between group size and vigilance. (a) Individual vigilance as a function of group size. Two possible relations are shown: the solid line shows a proportional reduction in per capita vigilance as group size increases; the dashed line shows no group size effect, i.e., animals maintain a constant level of individual vigilance independently of group size. (b) Total group vigilance as a function of group size. The solid line shows a constant total vigilance as a consequence of proportional reduction in individual vigilance with group size. The dashed line shows the corresponding total vigilance for no group size effect.

Relación entre tamaño de grupo y vigilancia. (a) Vigilancia individual en función del tamaño de grupo. Se muestran dos relaciones posibles: la línea sólida muestra una reducción proporcional en vigilancia per cápita a medida que aumenta el tamaño de grupo; la línea segmentada muestra ausencia de efecto de grupo, i.e., los animales mantienen un nivel constante de vigilancia individual independientemente del tamaño de grupo. (b) Vigilancia grupal total en función del tamaño de grupo. La línea sólida muestra vigilancia grupal constante como consecuencia de la reducción proporcional en vigilancia individual con el tamaño de grupo. La línea segmentada muestra la vigilancia grupal total en ausencia de efecto de grupo.

The exact relationship between group size and vigilance for a particular species is not straightforward. When there is no group size effect, per capita vigilance does not change with group size (Fig. 1a) and consequently, total group vigilance increases linearly with group size as a multiplying factor of solitary vigilance (Fig. 1b). If group members diminish their individual degree of vigilance proportionally to group size (Fig. 1a), then total group vigilance does not change with group size (Fig. 1b). For any given species with some degree of group size effect, the precise relation between vigilance and group size may lie somewhere between the two extremes already mentioned. Departures from those patterns may represent other factors that may interact with vigilance. For instance, a reduction in total vigilance with group size could be enhanced by a dilution effect (Hamilton 1971), where animals foraging in groups have lower probability of being preyed upon as group size increases, and hence individuals may allocate less time to vigilance than that expected in proportion to group size. Therefore, the particular relationship between vigilance and group size of a particular species is an empirical task.

In this study, I present observational results on vigilance and group foraging in the degu (*Octodon degus*, Molina 1752; Rodentia: Octodontidae), a caviomorph herbivorous rodent from central Chile. Direct field observations of degus are feasible because they are diurnally active (Fulk 1976, Yáñez & Jaksic 1978), and inhabit areas of open scrub vegetation with relatively low shrub cover (Bustos et al. 1977, Le Boulengé & Fuentes 1978, Zunino et al. 1992, Meserve et al. 1996). Commonly, degu populations dwell in large colonies comprising a system of underground galleries and surface runways (Fulk 1976, Yáñez & Jaksic 1978). Degus are common preys of raptors and foxes (Jaksic et al. 1993, Jaksic 1997), and they tend to bias above-ground activity to the vicinity of refuges (Jaksic 1986). The aim of the study was to assess the relationship between group size and vigilance and thus, test the predictions depicted in Figure 1. Given that the degu is highly social (Fulk 1976, Yáñez & Jaksic 1978, RA Vásquez, personal observation), the relationship between foraging activities and vigilance could give insight on the causes of sociality in this species. Although there is evidence that *O. degus* responds behaviorally to predation risk (Lagos et al. 1995), no aspect of sociality has been considered.

MATERIAL AND METHODS

The study was carried out between April and late July 1996 at the field station of the University of Chile, in a small canyon called Quebrada de la Plata, located in the coastal range 30 km west of Santiago (70°56'W, 33°29'S, 800 m a.s.l.). The degu population inhabits a xeric habitat of open

scrub vegetation at the origin of a large ravine. Shrub/tree cover is low (c. 10%), with *Quillaja saponaria, Acacia caven*, and *Trevoa trinervis* as dominant species. Herbs cover almost the entire area (c. 95%). The degu population occupies a system of underground burrows. Many burrow entrances are located in completely open habitat (lacking rocks and shrub/tree cover), and are connected above ground by a system of runways. Most of the observations were made from four different sites within a large area of c. 1 ha, that lacked shrub/tree vegetation.

Degus were observed foraging both as solitary individuals and as individual focal members in groups of 2-4 animals. Degus normally did not forage close to burrow openings, where they may engage in other displays such as agonistic interactions, play behavior, prolonged vigilance, resting, and burrow maintenance (Fulk 1976, Yáñez & Jaksic 1978). Therefore the observations on group foraging and vigilance were restricted to animals observed at > 3 m from burrow entrances and/or cover. When foraging, degus forage solitarily or in groups. Since there is a gradient in inter-individual distance between group members, ranging from completely isolated to close-together animals, I restricted my group observations to inter-individual distances of 1.5 m or less (see Martin & Bateson 1993). By referring to natural marks such as rocks and plants, I estimated the inter-individual distance between members of a foraging group (96.1 cm ± 5.2, mean ± SE, n = 40). Only 5% of foraging degus were observed at inter-individual distances < 0.5 m.

Observations were made between 8:00 and 17:00 h from four different naturally hidden places located underneath large trees and at > 30 m from focal animals. The behavior of focal animals was observed with 15-60X zoom binoculars. I collected data from focal animals observed during a continuous time period of 2-10 min. Data collection began 30 min after arrival at the hide. When an individual left or joined a focal group, data collection was interrupted. The time of occurrence of a particular behavioral transition was recorded with a stopwatch to the nearest second. Transitions between the following behaviors were recorded:

(1) Foraging: a crouching posture with the head lowered to ground level.

(2) Vigilance: two postures were observed; scanning, when only the head is raised from the feeding position, and upright, when in addition to head raising, the animal stand erect on its hind feet. This definition comprises Quenette's (1990) definition of vigilance: a motor action where there is a head lift with interruption of the ongoing activity followed by visual scanning of the surrounding environment.

(3) Running: quick movements between feeding positions and burrow entrances or runways. When running was observed, data collection for a given bout of activity was stopped.

Expenditure of time of focal individuals in groups of different sizes was examined to determine whether or not the time allocation to different activities is affected by group size. Following the criteria to observe foraging groups, observations of groups with five or more members was unusual. Therefore, the analysis comprises up to four-member groups.

Although it has long been recognized that vigilance may serve several functions (e.g., Dimond & Lazarus 1974), a majority of studies have considered it as an important anti-predator adaptation (Lima 1990). In its broad sense, as used in the psychological literature, vigilance means a general condition of enhanced ability to process information, implying a state of alertness directed towards certain stimuli (Dukas & Clark 1995). The behavioral postures assessed in the present study as vigilance are assumed to represent anti-predator adaptations.

Since data were not normally distributed, non-parametric statistics were used in most of the analyses (Spearman's rank correlation procedure). For multiple comparisons, I used Fisher's procedure of least significant differences with $\alpha = 0.05$ after a one-way ANOVA on log transformed data to meet the assumptions of the test.

RESULTS

Individual vigilance, expressed as the length of scanning events decreased with group size (Fig. 2a). Individual vigilance diminis-

hes 33.3% from solitary individuals to individuals in two-member groups, and the overall pattern, over the range of 1-4 individuals, is significant (r_s = -0.21, $p < 0.05$, n = 83). In particular, there is a large decrease from solitary individuals to groups of two animals, and a tendency to stabilize the length of per capita scanning events over the range of 2-4 individuals (one-way ANOVA on log transformed data, $F_{3,82}$ = 3.81, p = 0.013; Fisher's PLSD multiple comparison test shows significant differences between solitary animals and individuals in groups, but not among individuals from groups with two to four members). There is over a two-fold increase in mean feeding bout duration from solitary animals to individuals foraging in three-member groups (Fig. 2b), and the mean length of foraging bouts increased significantly with group size (r_s = 0.41, $p < 0.01$, n = 83). Although there is a conspicuous reduction in scanning time between animals foraging alone and in groups of two (Fig. 2a), there is no abrupt change in that transition of group size in terms of scanning rate (Fig. 2c). However, the reduction in scanning rate with group size was also significant (r_s = -0.34, $p < 0.01$, n = 83). By multiplying individual mean vigilance by the corresponding group size, I estimated total group vigilance. This calculation shows that total group vigilance increases with group size, and this increase lay between the predictions for no group size effect and constant total group vigilance (Fig. 3).

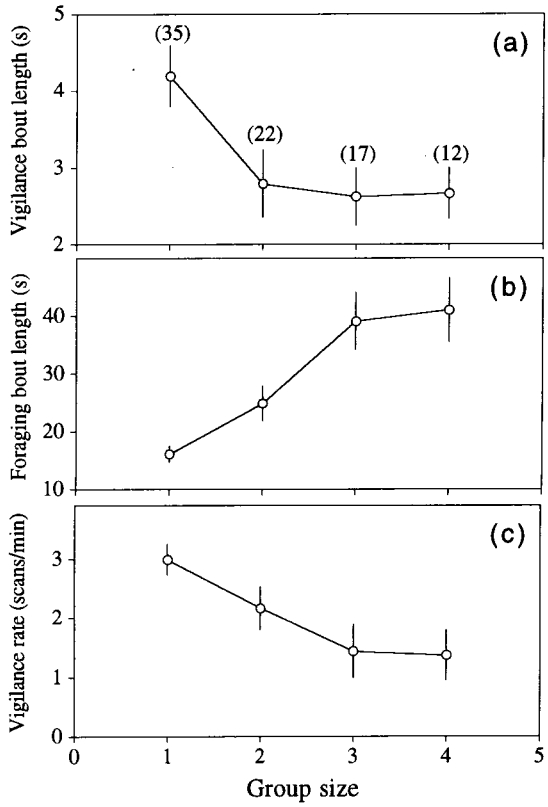

Fig. 2: (a) The relationship between vigilance bout length (mean ± SE) in seconds and group size. Numbers in parenthesis indicate sample size. (b) The relationship between foraging bout length (mean ± SE) in seconds and group size. (c) The relationship between vigilance rate (mean ± SE) in scans per seconds and group size.

(a) Relación entre la duración de los eventos de vigilancia (media ± EE) en segundos y el tamaño de grupo. Los números entre paréntesis indican el tamaño muestral. (b) Relación entre la duración de eventos de forrajeo (media ± EE) en segundos y el tamaño de grupo. (c) Relación entre la tasa de vigilancia (media ± EE) en "miradas" por minuto y el tamaño de grupo.

Some predation events were observed incidentally during the study, which may contribute to the knowledge of the natural history of the species. A black-chested buzzard eagle (*Geranoaetus melanoleucus*), dove suddenly towards a group of degus, and successfully captured one individual in its talons, immediately flying off with it, without using its beak. On another occasion, a culpeo fox (*Pseudalopex culpaeus*), abruptly rushed toward a burrow entrance where it caught a degu. During both these events, alarm calls were produced, and most of the degus fled to burrows, although many animals remained vigilant near burrow openings. Restoration of activity took about 10-20 minutes at the burrow closest to the attack. On another occasion, a burrowing owl (*Athene cunicularia*), was observed pulling along the ground a freshly killed dead degu into a burrow, although attack was not observed. Although many degus rested close to the safety of the burrow, some individuals close to burrow openings and not engaged in foraging were frequently observed in an alert posture (see also Yáñez & Jaksic 1978), possibly scanning the environment, in a position that resembles that of sentinels, commonly observed in other colonial species (Rubenstein & Wrangham 1988, Sher-

man 1977). Some of these degus emitted alarm calls when they appeared to detect a threat, and many of the nearby individuals fled to the burrow right after these alarms. These observations suggest that most members of a group are alerted once danger is detected by one group member.

DISCUSSION

Although degus do not normally form cohesive groups when foraging, they adjust their behavior similarly to other social feeding species. The individual level of vigilance decreased with group size, and this reduction resulted from degus making shorter and fewer scans. This differs from previous studies that have shown that many animals reduce scanning rate but not scanning bout length (e.g., Elcavage & Caraco 1983, Metcalfe 1984) or conversely, scanning bout duration but not scanning rate (e.g., Monaghan & Metcalfe 1985). The time saved from vigilance was allocated to foraging, as shown by the increase in mean length of foraging bout with group size. This foraging advantage is probably only in the short-term, otherwise I would expect foraging to be restricted only to group members and none to solitary individuals.

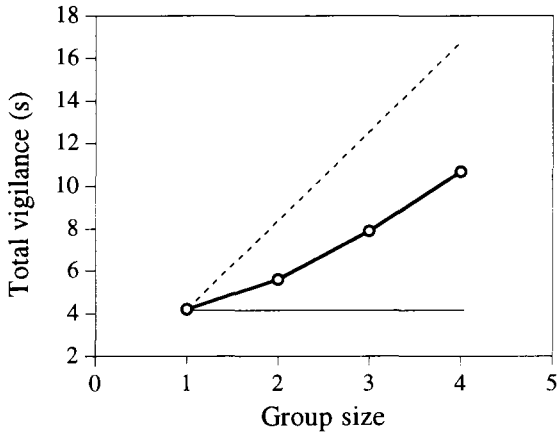

Fig. 3: The relationship between total group vigilance in seconds and group size (thick line). The dashed line shows the prediction for no group size effect, and the thin line shows the prediction for constant total vigilance. The data points have no dispersion indices because they were calculated from data on individual vigilance and group size (see Results).

Relación entre vigilancia grupal total en segundos y el tamaño de grupo (línea gruesa). La línea segmentada muestra la predicción para ausencia de efecto de tamaño de grupo y la línea fina muestra la predicción para vigilancia grupal constante. Los puntos no tienen índice de dispersión ya que fueron calculados a partir de vigilancia individual y tamaño de grupo (véase sección Resultados).

If all group members are immediately alerted once danger is detected, social foraging animals would take maximum advantage from vigilance by maintaining a total group vigilance similar to that of solitary individuals (see also Lima 1995a, 1995b). In this hypothetical case total vigilance should not increase with group size (Fig. 1b). Degus increase total vigilance with group size. Nevertheless, this increment lies below the predictions for a lack of group size effect. Presumably degus not only gain foraging advantages with increasing group size, but higher anti-predator benefits as well.

Vigilance may change not only with group size. The negative relationship between group size and individual vigilance may arise because other variables are correlated with group size and vigilance. Among the most important variables influencing vigilance and group size are: intragroup competition, position within the group, distance to cover/refuge, food density/quality, variability in foraging ability and physiological state (Elgar 1989, Lima & Dill 1990). Since degus form small groups and foraging groups were observed far from refuge, I do not expect competition, position within the group, and distance to refuge to have an important effect on the results of this study. Although my observation included only adult individuals and I have found low variability in vegetation density in the study site (dry biomass (mean ± SE) is 6.03 ± 1.29 g/100 cm^3, n = 20, with 72% of data in the range 3-8 g/100 cm^3), I cannot rule out food density and/or quality and inter-individual differences among degus as important factors affecting the degree of vigilance.

Anti-predator advantages are commonly considered as a major cause for group foraging and sociality (Wilson 1975, Pulliam & Caraco 1984, Rubenstein & Wrangham 1986). Although *O. degus* lives in social colonies (Fulk 1976, Yáñez & Jaksic 1978), its

exact degree of sociality is unknown. Anecdotal observations have described the use of alarm calls (Fulk 1976, Yáñez & Jaksic 1978, this study). Yáñez & Jaksic (1978) state that degus appear more alert when in open areas than when under cover. The degu colonies observed in the present study were located in an open area, barren of shrubs, trees, and rock piles. Close to burrow openings, degus were commonly observed being vigilant most of the time, in a sentinel-like position (see also Yáñez & Jaksic 1978). Alarm calls and sentinel behavior are common features of highly social birds and mammals (Rubenstein & Wrangham 1986), and in many cases these behaviors are related to kinship among members of the group, thus reflecting some sort of kin selection. A good example is found in ground squirrels, where the probability of emitting alarm calls is greater when a squirrel's neighbours are close kin (Dunford 1977, Sherman 1977). Whether kin selection has played an important role in the evolution of alarm calls in *O. degus* is unknown.

My observations revealed that when degus were vigilant they stopped other activities to engage in a more static alert posture which allowed visual scanning of the surroundings, and hence visual detection of dangerous events that occur unpredictably in the environment. Degus can discriminate between threat and non-threat events, and vigilance behavior may contribute to distinguishing these events. In this sense, there is evidence that degus do indeed discriminate between different raptor models, fleeing only when the model has the size of an actual predator (Yáñez & Jaksic 1978). This study shows that vigilance behavior in degus is facultative, that it may represent an anti-predator adaptation, and that it may have played an important role in degu social evolution. To understand fully the evolution and degree of sociality in this species, further studies on diverse aspects of social behavior should be undertaken.

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