Effect of Group Size on Individual and Collective Vigilance in Greater Rheas

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Abstract

We studied the effect of group size on the proportion of time that greater rheas, *Rhea americana*, allocated to vigilance and feeding during the non-breeding season. We tested whether: (1) the proportion of time that one bird allocates to vigilance (individual vigilance) decreases with group size, and (2) the proportion of time that at least one bird of the group is vigilant (collective vigilance) increases with group size. We analyzed video-recordings of birds that were foraging alone or in groups from two to 12 birds. The proportion of time allocated to individual vigilance decreased and the proportion of time spent feeding increased with group size. In both cases the main significant difference was between birds foraging alone and in groups. Collective vigilance did not vary with group size and it was lower than expected if vigilance bouts were random or sequential. Our results indicate that rheas foraging in large groups would not receive the benefit of an increase in collective vigilance, although they could still benefit from a reduction of predation risk by the dilution effect.

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Introduction

Living in a group provides members with potential benefits such as protection from predators, improvement in foraging and efficiency of energy expenditure and reproductive facilitation (Bertram 1980; Pulliam & Caraco 1984; Hammer & Parrish 1998; Ritz 1998).

One of the most widely studied benefits of living in groups is the decrease in the risk of predation. This benefit usually involves two different processes:

(1) a decrease in the individual probability of death during a predator attack (dilution effect, Hamilton 1971), and (2) an increase in the number of individuals that scan for potential predators (detection effect, Pulliam 1973). While the effect of dilution increases with the number of individuals in the group, the effect of detection depends not only on the size of the group, but also on how individual vigilance is organized within the group and how it varies with group size.

According to the detection effect hypothesis, if the individuals of the group scan at random, the probability of detecting a predator increases with group size. Therefore, individuals living in a group can reduce the proportion of time that they spend in vigilance and increase the time spent in other activities, such as foraging, without increasing the risk of predation. This benefit is known as the 'many-eyes effect' (Pulliam 1973) or 'collective detection effect' (Lima 1995). It is important to note that if scans are at random, individuals are likely to overlap their vigilance bouts as group size increases, which does not improve the probability of detecting a predator (Pulliam 1973).

In agreement with the 'many-eyes effect', several studies, mainly in birds and herbivorous mammals, have found that individual vigilance is negatively correlated with group size (see Bertram 1978; Pulliam & Caraco 1984; Lima & Dill 1990 for reviews). However, few of these studies have assessed whether collective vigilance varies with group size. Some studies estimated collective vigilance from individual vigilance, assuming that each animal in a group scans independently of one another (i.e. Monaghan & Metcalfe 1985; Yaber & Herrera 1994). Other studies measured collective vigilance but they were restricted to small groups (i.e. Bertram 1980; Quenette & Gerard 1992) or had a small sample size, precluding statistical analysis (i.e. Jarman 1987).

Individuals within a group can also raise their heads in a sequential manner, avoiding the overlapping of their scanning bouts (Ward 1985). This coordinated vigilance would involve costs to the members of the group, as each individual would be required to monitor the behavior of its companions (Ward 1985). The majority of the works that describe coordinated vigilance involve stable groups of individuals, mostly genetically related. Rasa (1986) found that vigilant captive mangooses, *Helogale undulata*, substitute for one another in a regular sequence. Similarly, McGowan & Woolfenden (1989) showed that Florida scrub jays, *Aphelocoma coerulescens*, have sentinels that coordinate their vigilance periods. Other authors (Ferrière et al. 1996, 1999) have found that in some birds, individual vigilance may entail non-random components that allow birds to coordinate their vigilance while reducing the costs of monitoring companions.

In this paper we assess the predictions derived from the detection effect hypothesis in greater rheas (*Rhea americana*). These large, flightless birds, spend a high proportion of the time foraging in open areas either alone or in groups of two to 50 individuals (Hudson 1920). In this species vigilance and feeding are not compatible behaviors (Reboreda & Fernández 1997). Rheas feed on grasses and insects that they find while walking slowly with their head held < 50 cm above the ground. Intermittently, they raise the head while looking around. Previous

studies have shown that individual vigilance decreases with group size (Martella et al. 1995; Reboreda & Fernández 1997) but these studies did not assess whether collective vigilance varied with group size and how vigilance bouts within a group were temporally organized. Here we analyze whether: (1) individual vigilance decreases with group size, thus increasing the time available for feeding, (2) collective vigilance varies with group size, and (3) individuals within a group scan independently (i.e. randomly) of each other, or sequentially (coordinated vigilance).

Methods

The study was carried out in two cattle ranches, 3500 and 800 ha in size, close to the town of General Lavalle, Province of Buenos Aires, Argentina (36°25′S, 56°56′W) during the 1995, 1996, and 1999 non-breeding seasons (Apr.–Aug.). The size of the population in our study area is approx. 400 rheas. Mean monthly temperatures during the study period varied from 8.1°C (Jul.) to 15.3°C (Apr.) while mean monthly rainfall varied between 50 and 150 mm. The habitat consisted of highly homogeneous pastures grazed by cattle. In these areas, there are no natural predators of adult rheas (i.e. cougar, *Felis concolor*), but rheas are hunted by feral dogs and occasionally by humans.

Data Collection

Every time we visited the study area and before starting the collection of data, we conducted a census in which we determined the total number of individuals and the size and sex composition of the groups. Rheas were considered to be part of a group if they were within 50 m of each other while they were considered to be solitary when no other rhea was within a radius of 100 m. We adopted this criterion because in all cases the distance to the nearest neighbor was either < 50 m (normally 10–30 m) or > 100 m. Group membership was not constant as rheas could leave and join the groups freely. However, the size of the group rarely changed during our observations and when this happened we stopped the recording of data. Rheas were video-recorded with a Sony Hi8 camcorder (Sony Corporation, Tokyo, Japan) from inside a vehicle at distances from 100 to 200 m. We started the video-recording 15–20 min after arriving at the place where the birds were foraging. They normally became accustomed to the presence of the vehicle within the first 5 min. Data were collected from 07:30 to 19:30 hours. Every day, we collected the data in a different place. As the birds were not marked and moved freely within the study area, repeated observations of the same birds may have occurred in some cases. However, if we recorded a bird more than once, it was on a different date or at a different place. Recordings ended after 10 min, or when the focal animal moved out of sight (behind a bush, tree, or another bird), any bird in the group was disturbed, or group size changed. We excluded recordings that lasted < 3 min. The average length of the recordings was 429.99 ± 151.27 s ($\bar{x} \pm$ standard deviation; n = 107; range 186.9–671.9 s).

Data analysis

The analysis of the videotapes was conducted with a computer running an event recorder program (Etholog 2.0). We employed focal-animal sampling to assess individual vigilance and all-animal sampling to assess collective vigilance (Lehner 1998). We analyzed individual vigilance from recordings of 107 birds that were foraging alone or in groups of two to 12 birds (n = 40). For each bird we measured the time allocated to vigilance, feeding, walking, and other behaviors (preening, resting, and aggressive interactions). As group size mainly affects vigilance and feeding and these activities represent approx. 80–90% of the daily time-budget of greater rheas (Reboreda & Fernández 1997), in this work we restricted the analysis to these behaviors. We also measured the length and the rate of the vigilance and feeding bouts. We considered a bird to be vigilant when it stood with its head up (including when the bird had its neck stretched or when the neck was forming an 'S' above its body).We considered a bird to be feeding when it had its head down and was pecking among the vegetation. As rheas walk almost continuously while foraging, we scored them as walking instead of feeding when the head was slightly above the body while walking.

To avoid pseudoreplication, we used the median of the individual records when we recorded more than one bird in a group. We calculated the proportion of time allocated to each activity. Proportions were arcsine-square root transformed to normalize the data (Shapiro–Wilk's W tests, W = 0.95, p = 0.15, for proportion of time spent in vigilance, and W = 0.99, p = 0.97 for proportion of time feeding). To analyze the effect of group size on feeding and vigilance, we used a multiple regression analysis, with proportion of time spent in vigilance and feeding as dependent variables, and group size, time of the day, and proportion of males in the group as independent variables. As the proportion of time spent in vigilance and feeding varied in a non-linear manner with group size, we used the inverse of group size. We chose this transformation because it provided a better fit to our data than did polynomial, negative exponential or linear models. Time of day (the time when birds were recorded) was incorporated as a linear term into the multiple regression model because we did not obtain a better fit using a polynomial (quadratic) regression model. The proportion of males in the group was arcsine-square root transformed to normalize the data. We analyzed variation in individual vigilance and feeding with group size using model – proportion of time spent in vigilance or feeding (arcsine-square root transformed data) $= a + b(1/N) + ct_d + dm$, where N is group size, t_d is the time of the day when the observation occurred, m is the proportion of males in the group (arcsine-square root transformed data), and a, b, c and d are the parameters of the regression. The mean lengths of feeding and vigilance bouts and their rate were analyzed using a similar multivariate model (with inverse of group size, time of the day, and proportion of males in the group as independent variables).

We also determined if there were differences in individual vigilance or feeding either between sexes or groups after controlling for the effect of group size. To evaluate sexual differences we compared the proportion of time spent in vigilance

or feeding in pairs of birds (one of each sex) that were foraging in groups of two to 8 individuals (n = 21 groups). For this comparison we used the residuals of the regression of proportion of time spent in vigilance (or feeding) vs. group size. Similarly, to determine if there were differences between groups, we randomly selected pairs of individuals of the same sex (n = 29 groups from two to 12 birds) from each group, and calculated the correlation between the pairs using the residuals of the regression of proportion of time spent in vigilance (or feeding) vs. group size.

We analyzed variation in collective vigilance from recordings of seven solitary birds and 49 groups from two to nine birds. For each recording we measured the proportion of time that at least one individual of the group was vigilant; the mean time that at least one individual remained head-up (length of vigilance bout); and the rate of these collective vigilance bouts. The observed value of the proportion of time that at least one individual of the group was vigilant was compared with the value expected if: (1) vigilance bouts were sequential, i.e. the scanning of one individual did not overlap with the scanning of other members of the group, and (2) vigilance bouts were random, i.e. the scanning of one individual was independent of the scanning of other members of the group (Bertram 1980; Quenette & Gerard 1992). To estimate the collective vigilance predicted by the sequential and random models for a given group size, we selected values of the proportion of time spent in vigilance at random from a normal distribution with a mean and standard deviation equal to the observed values for that group size (arcsine-transformed data). Collective vigilance predicted by the sequential model was estimated with the following formula:

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

where n is the group size, and V_i is the individual vigilance for each member of the group.

Similarly, collective vigilance predicted by the random model was estimated with the following formula:

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

where n is the group size, and V_i is the individual vigilance (Bertram 1980; Monaghan & Metcalfe 1985). To estimate the expected values for collective vigilance under the sequential and random models we performed 1000 simulations for each group size. We used confidence intervals of observed data to evaluate the differences between observed and predicted values.

Data are presented as $\bar{x} \pm$ SE. In Figs 1–3, we recalculated SE using arcsine transformation of the data and therefore they are not symmetrical about the mean.
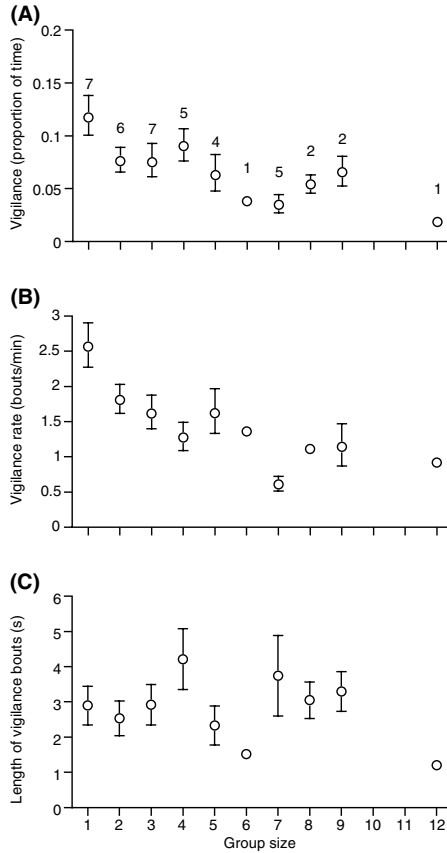
Fig. 1: Proportion of time allocated to vigilance (A), rate of vigilance bouts (B), and length of vigilance bouts (C) in greater rheas foraging alone or in groups from two to 12 birds. Numbers above error bars in A correspond to the number of birds recorded for each group size category

Results

Effect of Group Size on Individual Feeding and Vigilance

Rheas invested most of their time in feeding (79.8 ± 1.3%), vigilance (6.9 ± 0.4%) and walking between feeding patches (10.5 ± 0.9%). The remaining was used mainly in preening (2.4 ± 0.7%). Aggressive interactions and courtship displays involved on average < 0.2% of the available time.

Individual vigilance decreased with group size (Fig. 1A). The factors included in the regression model explained 31.2% of the variance (multiple regression analysis, $F_{3,36} = 5.44$, p < 0.003). There was a significant effect of group size on the proportion of time spent in vigilance ($t_{36} = 2.53$, p = 0.01) but there was no effect of time of the day or proportion of males in the group ($t_{36} = 0.42$, p = 0.81; and $t_{36} = 0.03$, p = 0.97, respectively). When we excluded solitary individuals from the analysis, we did not detect any significant effect ($F_{3,29} = 2.11$, p = 0.12),

although we observed a tendency for a decrease in individual vigilance with group size (partial regression coefficient, $t_{29} = 2.12$, $p = 0.04$).

The proportion of time that each bird spent in feeding increased with group size (Fig. 2A). The factors included in the regression model explained 43% of the variance (multiple regression analysis, $F_{3,36} = 9.25$, $p < 0.001$). There were significant effects of group size and time of day on the proportion of time that birds allocated to feeding ($t_{36} = 3.52$, $p = 0.001$; and $t_{36} = 2.54$, $p = 0.01$, respectively), but there was no effect of the proportion of males in the group ($t_{36} = 0.76$, $p = 0.45$). The effect of time of day remained when solitary individuals were excluded from the analysis ($t_{29} = 2.41$, $p = 0.02$), but no longer did we detect any effect of group size ($t_{29} = 1.18$, $p = 0.25$). We did not find any association between time of day and group size (Pearson product–moment correlation, $R = -0.14$, $Z = 1.20$, $p = 0.23$).
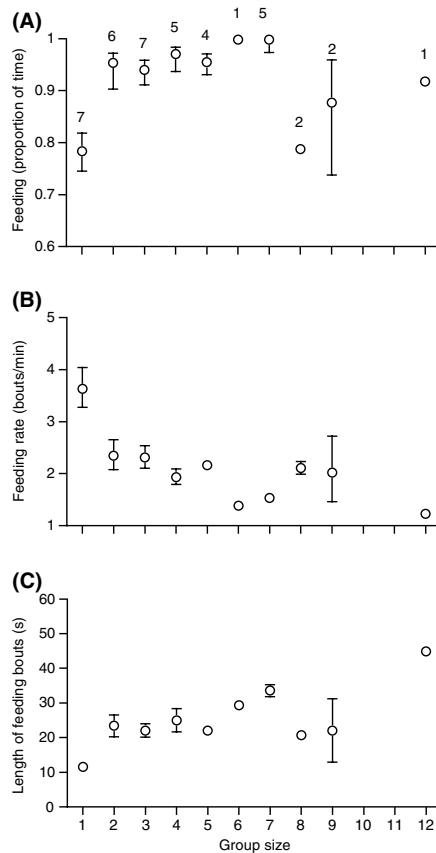

Fig. 2: Proportion of time allocated to feeding (A), rate of feeding bouts (B), and length of feeding bouts (C) in greater rheas foraging alone or in groups of two to 12 birds. Numbers below error bars in A correspond to the number of birds recorded for each group size category

The decrease in the proportion of time spent in vigilance with group size was the result of a decrease in the rate of vigilance bouts (partial regression coefficient; $t_{36} = 3.71$, $p < 0.001$; Fig. 1B), but there was no effect of group size on the length of the vigilance bouts (multiple regression analysis of mean length of scanning bouts; $F_{3,36} = 0.46$, $p = 0.71$; Fig. 1C). The increase in the proportion of time spent in feeding was the result of a decrease in the frequency (multiple regression analysis of feeding rate; $t_{36} = 3.91$, $p < 0.001$, Fig. 2B) and an increase in the length of feeding bouts ($t_{36} = 3.00$, $p = 0.004$, Fig. 2C).

Although there was a significant effect of group size on the proportion of time that rheas allocated to vigilance or feeding, the model explained only a small proportion of the variation of the data ($R^2 = 0.31$ and 0.43 for vigilance and feeding, respectively). Some of this variation could be explained by sexual differences. Males spent 7.9 ± 0.03% of the time vigilant and 79.5 ± 0.07% feeding, while the percentages for females were 4.6 ± 0.04 and 86.5 ± 0.05, respectively (Paired t-test, $t_{20} = 2.85$, $p = 0.01$ for vigilance and $t_{20} = 3.03$, $p = 0.006$ for feeding). Some of the variation could also be explained by differences between groups after controlling for the effect of group size. We found a positive correlation in the proportion of time allocated to vigilance between pairs of birds that were foraging in the same group (Pearson product–moment correlation, $R = 0.47$, $Z = 2.61$, $p = 0.009$). A similar correlation was observed for the proportion of time allocated to feeding (Pearson product–moment correlation, $R = 0.54$, $Z = 3.06$, $p = 0.002$).

Effect of Group Size on Collective Vigilance

The proportion of time that at least one individual of the group was vigilant did not vary with group size (simple regression analysis of proportion of time that at least one individual remained vigilant vs. group size^{-1}; $F_{1,55} = 2.3$, $p = 0.13$, $R^2 = 0.02$; Fig. 3A). The frequency and the average length of vigilance bouts were similar for all group sizes (simple regression analysis of length and rate of vigilance bouts vs. group size^{-1}; $F_{1,53} = 0.36$, $p = 0.55$, $R^2 < 0.01$, and $F_{1,53} = 0.05$, $p = 0.82$, $R^2 < 0.01$, respectively; Fig. 3B, C).

Collective vigilance in groups of three to eight birds was lower than predicted by both the random and sequential models (one-sample t test on squared-root transformed data; $p < 0.05$, for all comparisons; Fig. 3A).

Discussion

The benefits resulting from living in groups have been the focus of several theoretical studies derived from Pulliam's (1973) original model (e.g. Caraco 1979; Clark & Mangel 1986; McNamara & Houston 1992; Roberts 1996; Bednekoff & Lima 1998). These studies have shown that members of a group might benefit by reducing the amount of time spent in individual vigilance (and thus increasing the time available for feeding) without affecting the probability of detecting an
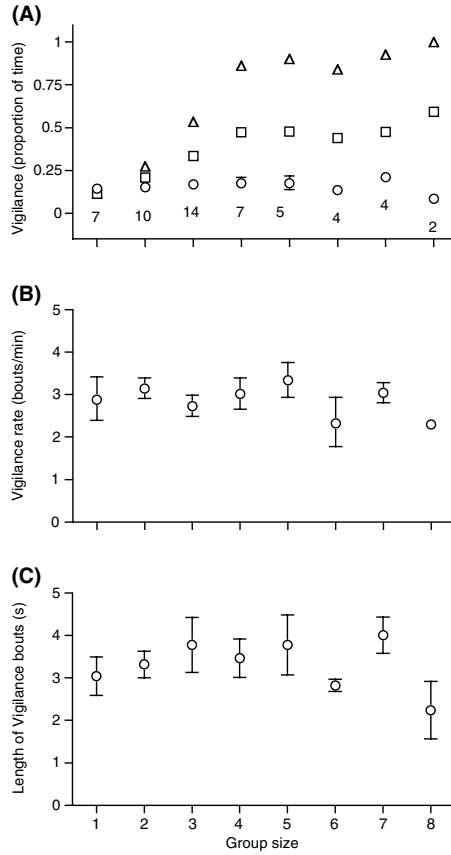
Fig. 3: (A) Variation in collective vigilance with group size. Values indicate the observed proportion of time that at least one bird of the group was vigilant (i.e. collective vigilance) (circles), the expected collective vigilance if vigilance bouts were at random (squares), and the expected collective vigilance if vigilance bouts were sequential (triangles). (B) Rate of vigilance bouts for the group. (C) Average length of the vigilance bouts for the group. Numbers below error bars in A correspond to number of records for each group size category

approaching predator. In agreement with these works, our results show that greater rheas foraging in groups allocate less time to vigilance and more time to feeding than solitary birds. Previous studies (Martella et al. 1995; Reboreda & Fernández 1997) also found that the percentage of time spent in individual vigilance was lower in groups than in solitary birds. These studies, as well as the present one, were conducted in very different habitats, which makes it unlikely that the results reflect an association between vigilance and habitat characteristics (Elgar 1989).

A common alternative hypothesis for explaining the negative correlation between group size and vigilance is that competition for food increases with group size and therefore, there is a positive correlation between feeding and group size

(and a negative one between vigilance and group size; Cézilly & Brun 1989; Elgar 1989; Lima et al. 1999). We did not detect significant differences in the proportion of time spent in feeding between individuals that foraged in groups of two to 12 birds. Rheas also might be responding in close proximity to another individual within the group, independently of its size, and therefore, they could increase the proportion of time feeding as a consequence of competition for food. However, if this were the case, we would expect a positive correlation between group size and feeding because proximity to another individual within the group should decrease with group size.

Another variable that might affect the level of vigilance is distance to cover (Elgar 1989). As the present study was conducted in a highly homogeneous habitat (open grasslands) we consider it very unlikely that this variable influenced our results.

Although there was a significant effect of group size on individual vigilance and feeding, our model explained only a small proportion of the total variation. Another source of variation was the difference in the proportion of time allocated to vigilance and feeding by males and females. In a previous work, we found sexual differences in vigilance and feeding in non-breeding groups, but these differences were attributed mainly to solitary individuals that were males (Reboreda & Fernández 1997). Also, Lombardi (1995) reported that males spent more time in vigilance than females during the breeding season, and attributed these differences to intrasexual competition and harem defense by males. Our data suggest that males maintain a higher vigilance level even during the non-breeding season.

A third potential source of variation was intrinsic differences between groups after controlling for group-size effects. Birds that were foraging in the same group showed a positive correlation in proportion of time allocated to vigilance or feeding. These differences between groups could be the result of spatial resource heterogeneity or perceived habitat risk. Groups foraging in rich (with high food abundance or quality) or safe areas would spend more time feeding and consequently, less time vigilant than groups in poor or risky areas.

Although the negative relationship between time spent in vigilance and group size has been widely shown, the assumption that group detection probability does not vary with group size has received less attention. This effect is based on the assumption that animals in a group scan for predators independently of each other, but this assumption has rarely been tested in the field. Bertram (1980) found that collective vigilance in ostriches (*Struthio camelus*) increases with group size, but his study was restricted to small groups (up to four individuals). He found that the observed pattern of vigilance did not differ from the one expected assuming that scanning was at random. Similarly, Quenette & Gerard (1992) found that collective vigilance in wild boar (*Sus scrofa*) increases with group size for small groups (two to three individuals) and then, decreases in larger groups, but these authors could not reject the hypothesis of individuals within groups scanning at random. Jarman (1987) also found that collective vigilance in groups of two or more kangaroos (*Macropus giganteus*) was higher than vigilance in

solitary individuals, but the small sample size precluded a statistical analysis of these differences.

Our results are consistent with Pulliam's model in that collective vigilance in large groups was not affected by group size. However, for most group sizes, collective vigilance departed from the expected value if birds in a group scan for predators at random or sequentially. We observed a low degree of organization of vigilance bouts within the group. Rheas in groups of two to eight birds showed a lower level of collective vigilance than expected if individuals had raised their heads randomly or sequentially. Possible explanations for this tendency toward simultaneous vigilance are that vigilance events can be elicited by specific stimuli of common interest or that a prolonged vigilance bout of one bird can elicit vigilance bouts of other birds of the group, thus producing a 'contagious behavior'.

Elgar et al. (1984) and Lima (1995) found that individuals responded to an attack more quickly when they were alert than when they were feeding and dependent on the vigilance of other members of the group, which would indicate that vigilance of other members of the group has lower value than an individual's own vigilance. This hypothesis could explain why animals maintain a certain level of alertness regardless of group size, but cannot explain why vigilance bouts in large groups were non-random. McGowan & Woolfenden (1989) suggested that there might exist an advantage in the existence of overlapping in vigilance as it could improve predator detection. Also, Fitzgibbon (1988) found that cheetahs (*Acinonyx jubatus*) prefer to attack non-vigilant Thompson's gazelles (*Gazella thompsoni*). Therefore, raising the head could also be a signal of alertness that affects the predator's decision to attack a prey. The simultaneous scanning of rheas foraging in large groups could reduce the chances of being selected as prey by an approaching predator. The results of such behavior would be a relatively high degree of simultaneous vigilance and the absence of any increase in collective detection.

Therefore, rheas that forage in large groups do not receive the benefit of an increase in collective vigilance. However, being a member of a large group could still reduce the risk of predation as a consequence of a dilution effect. Several studies have suggested that the effect of dilution becomes more effective as group size increases (Bertram 1980; Dehn 1990; Roberts 1996; Bednekoff & Lima 1998). Thus, for members of large groups, the failure in detecting a predator might have less effect on their probability of survival compared with solitary individuals or members of small groups.

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