

Effects of group size, habitat and hunting risk on vigilance and foraging behaviour in the Lesser Rhea (*Rhea pennata pennata*)

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Abstract. Gregariousness is a known anti-predator strategy, but factors other than the size of groups, such as the levels of predation pressure or habitat, can affect vigilance and foraging behaviour in birds. We studied the effects of group size, habitat (shrubland steppe v. meadows), and risk of hunting by humans (protected core area v. edge area exposed to poaching) on vigilance and foraging behaviour of wild populations of the Lesser Rhea (*Rhea pennata pennata*), a near-threatened ratite, in north-western Patagonia, Argentina. On average, Lesser Rheas allocated 18% of their time to vigilance and 67% to foraging. Individuals tended to be more vigilant with declining group size, in areas with low visibility that hinders escape by running, and in areas exposed to hunting, than in open habitats with abundant food or sites with low risk of hunting. Although time spent foraging was also influenced by habitat type and hunting risk, there was no direct relationship between foraging time and group size. As in other species of ratite, Lesser Rheas seem to take advantage of flocking as an anti-predation strategy. Our data do not only confirm the influence of group size, but also of habitat structure and hunting risk, in determining the behaviour of this flightless bird in the wild.

Additional keywords: anti-predation strategy, gregariousness, Patagonian steppe, ratite, time allocation.

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Introduction

Gregariousness is a strategy that allows members of a group to reduce individual vigilance without increasing the risk of being successfully attacked by a predator (Bertram 1978). Two main hypotheses have been proposed to explain the reduction in individual vigilance with increasing group size. The ‘dilution effect’ hypothesis suggests that the advantage of flocking lies in the reduction of individual predation risk, owing to an increasing number of individuals that are potential prey within a certain proximity (Hamilton 1971), whereas the ‘many-eyes’ hypothesis, proposes that the benefit of flocking lies in the distribution of vigilance effort among members of a group, because predators are collectively detected (Pulliam 1973). However, despite ample evidence supporting these hypotheses, some authors propose that variations in individual vigilance behaviour are also influenced by factors other than group size, such as predation pressure, habitat or food density (Elgar 1989; Roberts 1996; Beauchamp 2009).

The Lesser Rhea (*Rhea pennata pennata*) is a large flightless bird that inhabits Argentine Patagonia and southern Chile (Folch 1992) and has been categorised as ‘near threatened’ globally in the International Union for Conservation of Nature Red List of Threatened Species (BirdLife International 2011). The two natural predators of this ratite in north-western Patagonia are the Puma (*Puma concolor*), which is more likely to attack adult Rheas, and the Culpeo, or Andean Fox (*Pseudalopex culpaeus*),

which mainly preys on eggs and chicks (Novaro *et al.* 2000), but both are almost absent in the study area (F. R. Barri, pers. obs.). At present, humans are the main predator of the Lesser Rhea, which is taken by local people for its meat, leather and eggs (Martella and Navarro 2006). Consequently, hunting and loss of habitat are the most important factors affecting wild populations of Lesser Rhea in Patagonia (Barri *et al.* 2008, 2009a). This gregarious species forms groups of a few to 40 or more birds, and has a complex reproductive system that combines polygyny with sequential polyandry (Handford and Mares 1985), in which the male incubates and takes care of the precocial chicks for 2–3 months after hatching (Barri *et al.* 2009b).

Lesser Rheas are primarily herbivorous (Bonino *et al.* 1986). The Patagonian steppe comprises two habitats of differing vegetation structure: shrubland and grassy meadows (locally known as ‘mallines’) with less vegetation than the shrubland. Mallines occupy a fairly small portion of the Patagonian region, but are one of the most highly productive areas (León *et al.* 1998) and are a preferred habitat of Lesser Rheas for foraging and breeding (Bellis *et al.* 2006; Barri *et al.* 2009b).

Studies on vigilance and foraging behaviour have been carried out in species closely related to the Lesser Rhea. In the Greater Rhea (*Rhea americana*) individual vigilance is greater in habitats with low visibility, where early detection of predators and escape by running are hindered (Martella *et al.* 1995; Codenotti and

Álvarez 2000). The same trend has been observed in other species of ratite, such as the Ostrich (*Struthio camelus*) and the Emu (*Dromaius novaehollandiae*) (Bertram 1980; Boland 2003). In the Greater Rhea, flocking has been suggested as a strategy to reduce predation risk, as it would increase the probability of detecting potential predators (Martella *et al.* 1995; Carro and Fernández 2009). Conversely, hunting pressure has been shown to induce changes in vigilance and foraging behaviour in other herbivorous prey species (e.g. Benhaiem *et al.* 2008), but the effect of hunting risk on the behaviour of rheas has still not been evaluated.

Despite their importance, there have not been any detailed behavioural studies of Lesser Rhea in the wild. The aim of the present work was to examine vigilance and foraging behaviour of a wild population of Lesser Rhea in the Patagonian steppe. We hypothesised that the time allocated to vigilance and foraging would vary not only with group size but also with habitat and hunting risk. Accordingly, we expected Rheas to spend less time in vigilance and more time in foraging with increasing group size and with the use of open habitats, such as mallines, and of areas of lower hunting risk.

Materials and methods

We studied the time allocated to vigilance and foraging behaviour by wild Lesser Rheas during two successive reproductive seasons (August–March 2004–05 and 2005–06) on a ranch of the Instituto Nacional de Tecnología Agropecuaria (INTA) Bariloche, Río Negro province, Argentina (41°07'43"S, 71°15'06"W; 775 m above sea level). This 7800-ha ranch is located in north-western Patagonia and comprises two distinct habitats: shrublands, dominated by *Mulinum spinosum* and *Nassauvia glomeruli*, with vegetation 60–80 cm tall; and mallines, with cover of short (<30 cm) grasses dominated by *Juncus balticus* and *Festuca palllescens* (Bonino *et al.* 1986). Food density does not seem to be a limiting factor for Lesser Rheas (Bonino *et al.* 1986).

On the ranch, where the main activity is extensive sheep production using sustainable land-management practices, wild Lesser Rheas occur at a density of 1.7 Rheas km⁻² and are actively protected. On neighbouring ranches, however, the species is subjected to moderate to intensive hunting and densities are lower (range: 1.3–0.3 Rheas km⁻²) (Barri *et al.* 2008). For Lesser Rheas on the experimental ranch, the risk of encounters with hunters increases as Lesser Rheas approach the boundaries of the property because they can be more easily spotted and shot both from neighbouring ranches and the provincial Route 23, which runs along one side of the experimental ranch (see a map of the study area in Barri *et al.* 2008).

We conducted observations between 0700 and 1900 hours over an average of 46 days for each successive reproductive season. Observation sites were sampled randomly (by choosing a random cardinal point within the study area before conducting each ground survey) at locations that were far enough from one another (>1000 m) to avoid repeated observations of the same individual. For each group of Lesser Rheas detected, we recorded individual behaviour (following the procedure described below), number of individuals, type of habitat (mallines *v.* shrubland steppe) and relative location in the field (core *v.* edge area). The edge area, which is the area with greatest hunting pressure, was

defined as the 300-m strip internal to the boundary of the experimental ranch, based on: (1) the average distance at which Lesser Rheas detected our presence in the study area; (2) the approximate maximum range for an average hunter to spot and accurately shoot an animal from the provincial Route 23; and (3) a reasonable distance at which an unalarmed Rhea could avoid predation by hunters or their dogs, who can intrude on the protected ranch either from the highway or the neighbouring ranches.

We classified the individual Rheas observed into the following categories: male with chicks (in which only one pair of eyes is effectively vigilant); solitary individuals (when no other adult individual was detected within a 100-m radius); and groups (range observed: 2 to 14 individuals). Because the species does not show strong sexual dimorphism, sex was not included in the analysis (except for males with chicks).

Observations were made using focal-animal sampling (Lehner 1996), using a 15–60 × 60-mm telescope (Hokenn, Buenos Aires, Argentina). Behavioural data were recorded on a tape recorder (Nokia, Buenos Aires, Argentina) and time measured with a digital stopwatch. The range of distances between the observer and the focal animals were 100–300 m, and the observer started to collect data 10 min after arriving at the site to avoid effects of initial approach on the behaviour of the Lesser Rheas. For each group observed, a maximum of four individuals were selected randomly, following a protocol established for such behavioural studies (Lehner 1996). Two 10-min focal samples of behaviour, with a 15-s interval between samples, were obtained for a single individual before going on to next animal in the group. Focal observations lasting <3 min were discarded. Recording was interrupted only if the sampled individual was out of the observer's sight or when the distance was not enough to record behaviour properly (>50 and <300 m). We conducted an average of ~35 hours of focal observations for each reproductive season.

Using the criteria of Raikow (1968), and used by Martella *et al.* (1995) and Carro and Fernández (2008, 2009), we classified an individual as 'vigilant' when it was standing with its head held above the body, with the neck stretched up or back into an 'S' curve; and as 'foraging' when, either standing or moving slowly, it held the head below a horizontal line through the mid-body.

For each focal sample, the proportion of total time each Lesser Rhea allocated to vigilance and foraging behaviours was calculated. Proportions were arcsine-transformed and normality verified using the Shapiro-Wilks test. To avoid subsample inference, data for individuals within each group were averaged. The effect of group size, habitat and field site on time devoted to foraging and vigilance behaviour was analysed with a nested, multifactorial analysis of variance (ANOVA) with contrasts between levels of the categorical variables at a fixed group size. After that, *a posteriori* comparisons were made with a Fisher test (Least Significant Difference), including a dummy variable to determine possible differences between solitary individuals and males with chicks.

Results and discussion

On average, Lesser Rheas devoted 18 ± 2% (s.e.) of their time to vigilance, 67 ± 11% to foraging, and the rest (15 ± 3%) to other behaviours, such as preening and resting. The average proportion

of time an individual allocated to vigilance decreased with increasing group size ($R^2=0.41$, $P=0.010$), and males with chicks devoted more time to vigilance than solitary individuals ($P=0.031$). Conversely, time allocated to foraging did not increase linearly with increasing group size ($R^2=0.16$, $P=0.137$), and no differences between males with chicks and solitary individuals ($P=0.120$) were observed (Fig. 1).

It thus seems that Lesser Rheas flock because of the advantages they obtain from group vigilance, as observed in other ratites, such as the Greater Rhea (Martella *et al.* 1995; Carro and Fernández 2008, 2009), Ostrich (Bertram 1980) and Emu (Boland 2003). Group vigilance provides individuals with greater chances of detecting predators, as reported for the Greater Rhea (Lombardi 1994; Martella *et al.* 1995; Carro and Fernández 2009). Nonetheless, males with chicks allocated the greatest proportion of time to vigilance. Although these groups may have many members, they may be more vulnerable to attack by

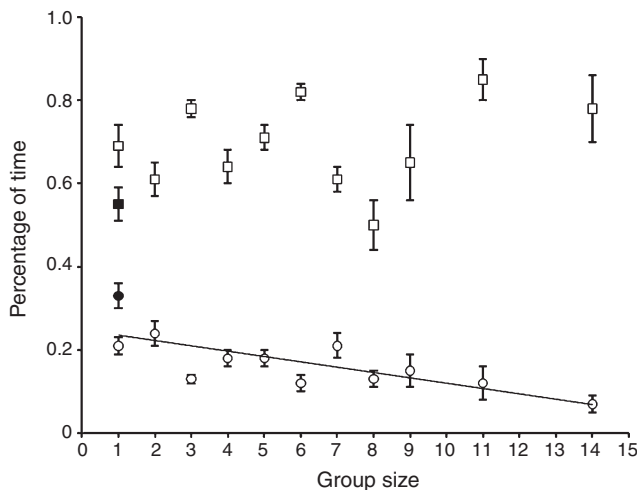


Fig. 1. Allocated percentage of time to vigilance (circles) and foraging behaviour (squares) in relation to group size in wild Lesser Rheas (mean proportion of time \pm s.e.). Solid symbols indicate groups composed of an adult male with chicks (where only the adult male is considered vigilant).

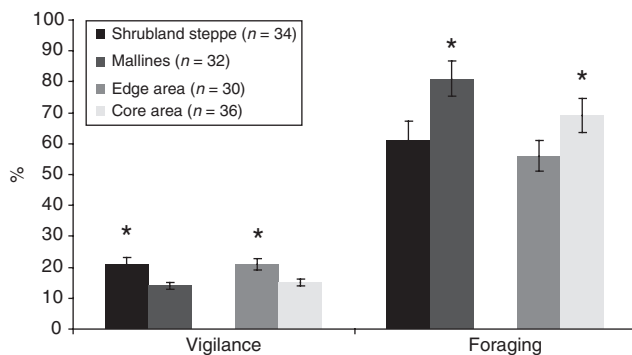


Fig. 2. Mean proportion of time allocated to vigilance and feeding behaviour (% \pm s.e.) in relation to habitat and hunting risk in wild Lesser Rheas. Significant differences at $P < 0.05$ in a *posteriori* comparison Fisher's Least Significant Difference test are marked with asterisks.

predators, because only the adult male is effectively vigilant (Barri *et al.* 2009a).

Interestingly, allocation of time to vigilance and foraging was not only influenced by group size ($F=6.57$, $P < 0.001$; $F=2.37$, $P=0.017$), but also by habitat and field site. Indeed, individuals allocated more time to vigilance in shrubland steppe than in mallines, and more time in the edge area than in the core area. Conversely, individuals allocated less time to foraging in the shrubland steppe than in the mallines, and less time in the edge area than in the core area (Fig. 2). These results suggest that vigilance in this species may be a factor not only of group size, but also of other ecological factors, such as anthropogenic disturbances and habitat. This is in agreement with a meta-analysis that provided evidence supporting the relationship between group size and time allocated to vigilance, although a large amount of variation in vigilance was unexplained (Beauchamp 2008).

The influence of habitat structure and hunting risk on vigilance and foraging behaviour contributes to our understanding of the Lesser Rhea's preference for open habitats, as reported by Bellis *et al.* (2006) and Barri *et al.* (2009b). Selecting habitats that combine high food quality and availability of food with good visibility, such as mallines, seems to be a typical behaviour of ratites (Milton *et al.* 1994; Codenotti and Álvarez 2000; Bellis *et al.* 2006). Conversely, predation pressure exerted by poaching, which is frequent in the edge area, also appears to be a significant factor influencing time allocated to vigilance and foraging by Lesser Rheas. Indeed, Barri *et al.* (2008) showed that hunting is the most important factor affecting species survival in the study area. Besides reducing population size directly, hunting pressure probably affects animal welfare indirectly in terms of energetic balance, as the Lesser Rhea needs to invest more time to vigilance at the expense of other important behaviours, such as foraging.

The present study provides the first evidence of the influence of group size, habitat and hunting risk on vigilance and foraging behaviour of the Lesser Rhea in Patagonia, and stresses the importance of preserving mallines and protecting areas from hunting for the conservation of Lesser Rheas in the Patagonian steppe.

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