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Sexual, Seasonal and Group Size Differences in the Allocation of Time between Vigilance and Feeding in the Greater Rhea, *Rhea americana*

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Abstract

We studied the effect of sex and group size on the proportion of time a greater rhea, *Rhea americana*, allocates to vigilance and feeding during the breeding and the non-breeding seasons. We analysed 175 records of focal animals that were feeding alone or in groups of 2 to 26 birds. In both seasons, males spent more time in vigilance and less time in feeding than females. Both sexes spent more time in vigilance and less time in feeding during the breeding season. Sexual and seasonal differences in vigilance were the result of different mechanisms. Males had shorter feeding bouts than females but there were no sexual differences in the length of the vigilance bouts. On the contrary, seasonal differences were the result of males and females having longer vigilance bouts during the breeding season but there were no seasonal differences in the length of the feeding bouts. During the non-breeding season, individual vigilance was higher in rheas foraging alone than in groups. In this case, solitary birds had longer vigilance and shorter feeding bouts than birds foraging in groups. We discuss the possible effect of intragroup competition and food availability on the allocation of time between feeding and vigilance in this species.

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Introduction

Time is a limited resource which animals have to allocate between different behaviours. One of the decisions they must make is how much time to assign to vigilance and feeding. In most species, vigilance is incompatible with feeding and therefore high rates of energetic gain could only be achieved at the cost of increasing the risk of predation. One form of decreasing the risk of predation without affecting energetic gain is living in a group. Individuals in a group may benefit from the vigilance of companions and therefore each individual can decrease its own vigilance, and consequently increase the time spent feeding, without affecting the probability of

detecting a predator (detection effect, PULLIAM 1973). In agreement with the detection-effect hypothesis, several studies (mainly in birds and herbivorous mammals) have found that individual vigilance is negatively correlated with group size (reviews: BERTRAM 1978; PULLIAM & CARACO 1984; LIMA & DILL 1990). Several variables other than group size could also affect the amount of time devoted to vigilance (ELGAR 1989). These variables are, among others, density or type of food resource (BARNARD 1980; LAWRENCE 1985), intragroup competition (CARACO 1979; MONAGHAN & METCALFE 1985; ELGAR 1987), position in the group (JENNINGS & EVANS 1980; INGLIS & LAZARUS 1981), sex (BERTRAM 1980; WAITE 1987; HOGSTAD 1988) or breeding status (SULLIVAN 1988).

    In this paper we explore the allocation of time between vigilance and feeding in the greater rhea, *Rhea americana*. Greater rheas are large (males up to 40 kg, females up to 30 kg) flightless birds that spend a high proportion of their time seeking and eating in open grasslands. In this species, vigilance and feeding are incompatible behaviours. Rheas feed on leaves and insects that they find while walking slowly with the head to less than 50 cm of the ground. Intermittently, they raise the head and remain still with the neck fully erect while looking around. When they are in this position the head is at a height of over 1.5 m. During the non-breeding season, rheas forage both alone and in groups of 2 to 50 birds (HUDSON 1920). These winter flocks start breaking up at the beginning of the breeding season when there are aggressive encounters between adult males (HUDSON 1920). By the onset of the breeding season, the social structure of a greater rhea population consists of single males, reproductive groups (harems) of 1 or 2 males with 2–15 females and large flocks of yearlings with non-reproductive adults (BRUNING 1974).

    Two previous studies addressed the allocation of time to vigilance in greater rheas. LOMBARDI (1994) found that during the reproductive season, males with a harem allocate more time to vigilance and less time to feeding than the harem females. In this work, the effect of group size on vigilance was not analysed but males with harems were as vigilant as solitary males. In another study, MARTELLA et al. (1995) found that during the non-breeding season, the percentage of time spent in vigilance decreased as group size increased, but they did not find sex differences in vigilance. As these studies were conducted in different habitats and during different seasons, the discrepancy between them could be the consequence of vigilance being influenced by these variables. To avoid these confounding variables, we studied the effect of sex and group size on the allocation of time between vigilance and feeding during the breeding and the non-breeding season for the same rhea population.

Methods

    The study was carried out in the province of Entre Ríos, Argentina (33°01'S, 58°24'W), in a 7000-ha cattle ranch (Estancia Ñandubaizal) where there is a natural population of approximately 150 greater rheas, with a similar proportion of males and females. The habitat consisted of open grasslands with scattered patches of trees and bushes. In our study site, adult rheas do not have natural predators (i.e. cougars, *Felis concolor* and jaguars, *Felis onca*) at present, but they are still hunted regularly by humans and feral dogs.

We collected the data in Oct.–Nov. 1991 and 1992 (breeding season) and Jul.–Aug. 1992 (non-breeding season). The first courtship activities (i.e. wing display, RAIKOW 1969) started in late Sep.–early Oct. and the first eggs were laid in mid Oct. Last hatching occurred in late Dec.–early Jan.

We observed focal animals while they were feeding alone or in groups of 2 to 26 birds (non-breeding season) or 2 to 16 birds (breeding season). Rheas were considered to be solitary when no other rheas were within 100 m whereas they were considered to be part of a group if they were within 50 m of one another. Usually, individuals in groups were 10–40 m apart, and in most cases, solitary individuals had no companions within 300 m. We analysed 175 focal records, 81 collected during the breeding season (29 females and 52 males) and 94 during the non-breeding season (29 females and 65 males). In the analysis we did not include records of juveniles (less than one year old) because previous observations showed that they were consistently associated with large groups. Neither did we include records of males with chicks because they spend significantly more time on vigilance than solitary individuals or birds in groups.

Observations were made with 12 × 50 binoculars, from inside a vehicle at distances of 100 to 300 m from the groups. We started to record the data 15 min after arriving at the place where the birds were foraging. They got used to the presence of the vehicle within the first 5 min. Data were collected from 0730 h to 1930 h. Every day, we recorded the data in a different place. Because the birds were not marked and moved freely within the study area, repeated observations of the same bird cannot be excluded. However, if we observed a bird more than once, it was on a different date or at a different place.

We measured the time a bird allocated to vigilance, feeding, walking, preening, resting, courtship and to aggressive interactions. Measurements were made with a portable computer running an event-recorder program. We considered that a bird was vigilant when it stood with its head up, and that it was feeding when it had the head down and was pecking among the vegetation. Because rheas walk almost continuously while foraging, we considered that they were walking instead of foraging only when the head was above the body while walking. A record of a focal animal ended after 15 min of observation or when the animal moved out of sight (behind a bush, tree or another bird). We excluded records that lasted less than 3 min. The average length of our records was 658.5 ± 16.5 s ($\overline{X}$ ± SE).

Data from the observation period of each focal bird were used to calculate the percentage of time allocated to different behaviours. Because the arcsin transformation failed to normalize our data (Shapiro–Wilks' W-test, $p < 0.05$ for vigilance and $p < 0.001$ for feeding), non-parametric statistics were used. For the analysis of group size effect, we pooled the data of different group sizes in the following categories: solitary birds, groups of 2 birds, groups of 3–4 birds, groups of 5–8 birds, groups of 9–16 birds, and groups of more than 17 birds. For the analysis of the bout lengths, we calculated the mean of the vigilance and feeding bouts of each focal bird. We only considered those birds with at least 2 sequences of feeding–vigilance or vice versa.

Results are $\overline{X}$ ± SE.

Results

Sexual and Seasonal Differences in Time Allocation

We compared the percentage of time males and females allocated to different behaviours during the breeding and the non-breeding season. Males spent more time in vigilance and less time in feeding than females, both during the breeding (Mann–Whitney U-test, $z = -2.58$, $p = 0.0099$ for vigilance and $z = -2.57$, $p = 0.01$ for feeding) and the non-breeding season (Mann–Whitney U-test, $z = -3.57$, $p = 0.0004$ for vigilance and $z = -2.00$, $p = 0.045$ for feeding). During the breeding season, both sexes spent more time in vigilance (Mann–Whitney U-test, $z = -2.70$, $p = 0.0068$ for males and $z = -2.95$, $p = 0.0032$ for females) and less time in feeding (Mann–Whitney U-test, $z = -3.58$, $p = 0.0003$ for males and $z = -2.43$, $p = 0.015$ for females) (Fig. 1). There were neither sexual nor seasonal differences in the time allocated to walking, preening or resting.

The sexual and seasonal differences in vigilance were the result of different mechanisms. Males had shorter feeding bouts than females, both during the breeding
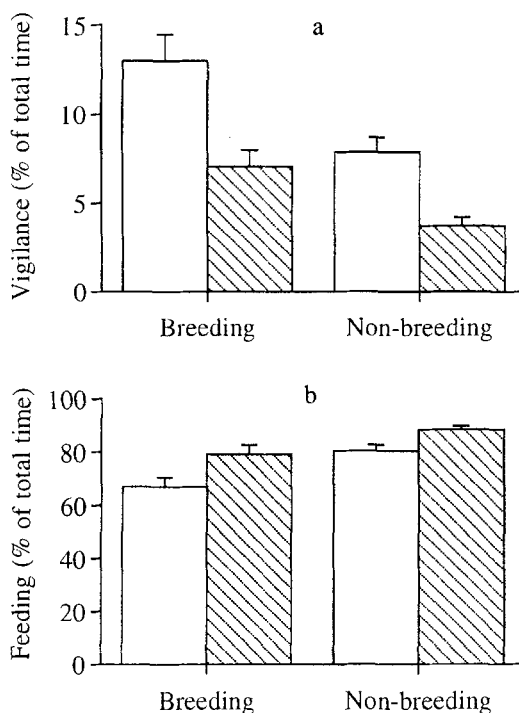
Fig. 1: Percentage of time ($\overline{X} \pm$ SE) allocated to vigilance (a) and feeding (b) by males (empty bars) and females (striped bars) during the breeding and the non-breeding season. The numbers of focal birds observed were 52 males and 29 females during the breeding season and 65 males and 29 females during the non-breeding season

(Mann–Whitney U-test, $z = -2.34$, $p = 0.019$) and the non-breeding season (Mann–Whitney U-test, $z = -4.34$, $p = 0.0001$), but there were no sexual differences in the length of the vigilance bouts, either in the breeding (Mann–Whitney U-test, $z = -0.7$, $p = 0.48$) or in the non-breeding season (Mann–Whitney U-test, $z = -1.44$, $p = 0.15$). On the other hand, the seasonal differences within sexes were the result of an increase in the length of the vigilance scans. Both males and females had longer vigilance bouts during the breeding than during the non-breeding season (Mann–Whitney U-test, $z = -3.67$, $p = 0.002$ for males and $z = -3.68$, $p = 0.0002$ for females), but there were no seasonal differences in the length of the feeding bouts (Mann–Whitney U-test, $z = -0.32$, $p = 0.75$ for males and $z = -1.31$, $p = 0.19$ for females) (Fig. 2).

Because solitary birds are more vigilant than birds in groups (see below) and in most cases solitary birds were males, the sexual differences in vigilance could be the result of a confounding effect of group size. To test this hypothesis, we repeated the previous analysis with males and females that were foraging in groups of 5–8 birds.
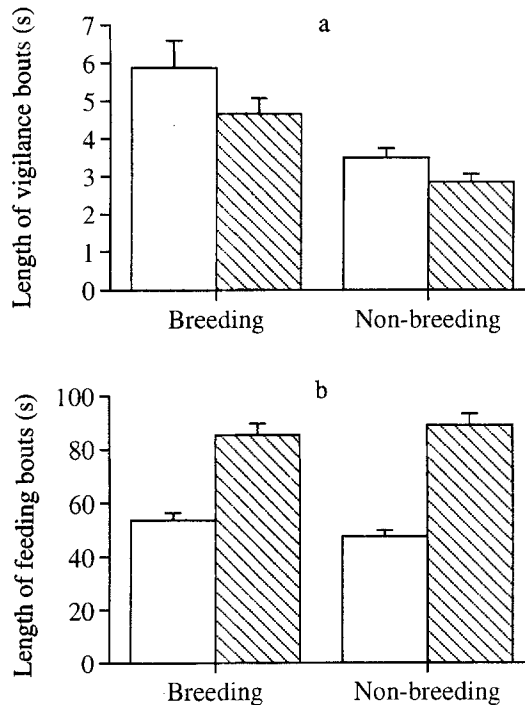
Fig. 2: Length ($\overline{X} \pm$ SE) of the vigilance (a) and feeding (b) bouts of males (empty bars) and females (striped bars) during the breeding and the non-breeding season. The numbers of birds analysed were 49 males and 28 females during the breeding season and 54 males and 29 females during the non-breeding season

Males spent more time in vigilance and less time in feeding than females (Mann–Whitney U-test, z = −3.15, p = 0.002 for vigilance and z = −2.26, p = 0.02 for feeding) and the sexual differences were the result of males having shorter feeding bouts than females (Mann–Whitney U-test, z = −3.28, p = 0.001).

Group Size Effect on Vigilance

We analysed the percentage of time allocated to vigilance by males and females that foraged alone or in groups of different sizes. During the non-breeding season, there was a clear effect of group size on vigilance (Kruskal–Wallis H = 20.97, p = 0.0008). Vigilance in solitary birds was significantly higher than vigilance in birds that were foraging in groups (p < 0.05 for all comparisons). However, the percentage of time spent in vigilance did not vary between birds foraging in groups from 2 to 26 individuals (Fig. 3). The effect of group size on vigilance was significant in males (Kruskal–Wallis H = 16.20, p = 0.006) but not in females (Kruskal–Wallis H = 7.48, p = 0.187).

During the breeding season, the effect of group size on vigilance was weaker than in the non-breeding season (Kruskal–Wallis H = 8.88, p = 0.064). Vigilance in males
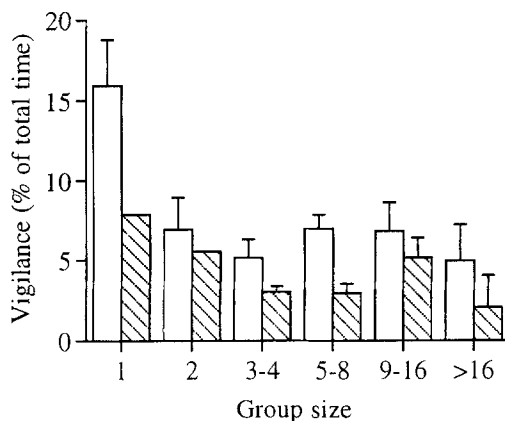
Fig. 3: Percentage of time ($\overline{X} \pm$ SE) allocated to vigilance by males (open bars) and females (striped bars) during the non-breeding season when they were foraging alone or in groups. The number of focal birds observed for each group size was: solitary birds, 10 males and 1 female; groups of 2, 11 males and 1 female; groups of 3–4, 10 males and 6 females; groups of 5–8, 19 males and 11 females; groups of 9–16, 11 males and 8 females; and groups of more than 16 birds, 4 males and 2 females

foraging in groups was as high as in solitary males (Kruskal–Wallis H = 1.91, p = 0.75). In females, vigilance was higher in solitary birds or birds in groups of 2 than in birds in groups bigger than 2 (Kruskal–Wallis H = 10.59, p = 0.014) (Fig. 4).

To understand the causes of the group size differences in vigilance during the non-breeding season, we compared the length of the vigilance and feeding bouts in solitary males and in males that were foraging in groups of 2. Solitary males had longer vigilance and shorter feeding bouts than males foraging in groups of 2 (Mann–Whitney U-test,
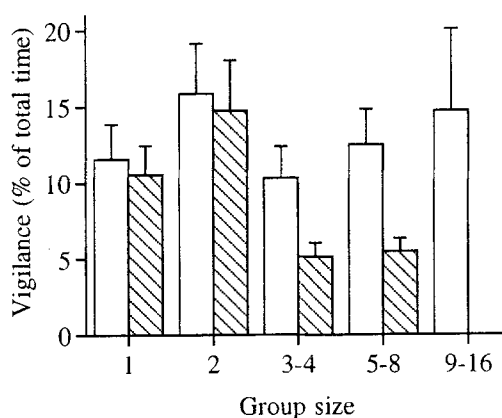

Fig. 4: Percentage of time ($\overline{X} \pm$ SE) allocated to vigilance by males (open bars) and females (striped bars) during the breeding season when they were foraging alone or in groups. The number of focal birds observed for each group size was: solitary birds, 7 males and 3 females; groups of 2, 8 males and 3 females; groups of 3–4, 7 males and 8 females; groups of 5–8, 20 males and 15 females; groups of 9–16, 10 males
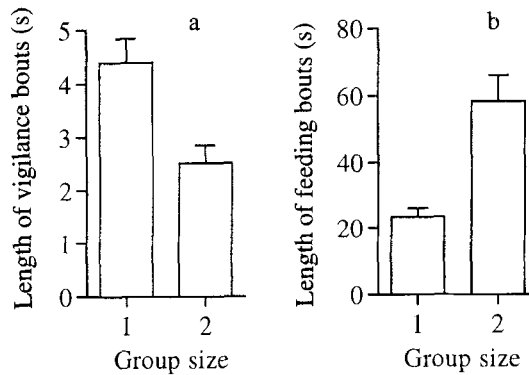
Fig. 5: Length ($\overline{X} \pm$ SE) of vigilance (a) and feeding (b) bouts in males foraging alone (n = 9) or in groups of 2 (n = 9) during the non-breeding season

$z = -2.78$, $p = 0.0054$ and $z = -3.22$, $p = 0.0013$ respectively) (Fig. 5). This result was the consequence of a different length-frequency distribution of the vigilance and feeding bouts. Solitary birds had a lower proportion of vigilance bouts shorter than 4 s, and a higher proportion of vigilance bouts longer than 4 s, than birds in groups of 2 (Kolmogorov-Smirnov test, $p = 0.0001$). The opposite trend was observed in the frequency distribution of the feeding bouts. In this case, solitary birds had a higher proportion of feeding bouts shorter than 30 s, and a lower proportion of feeding bouts longer than 30 s, than birds in groups of 2 (Kolmogorov–Smirnov test, $p = 0.0001$).

Discussion

Sexual and Seasonal Differences in Time Allocation

Sexual differences in vigilance during the breeding season were observed previously in rheas (LOMBARDI 1994) and in ostriches (BERTRAM 1980; BURGER & GOCHFELD 1988). LOMBARDI (1994) found that male rheas with a harem were more vigilant than females in a harem and suggested that these differences could be the result of males investing more time in vigilance to retain the females already recruited. Similarly, BURGER & GOCHFELD (1988) pointed out that in ostriches, sexual differences in vigilance could be the result of males competing for females. Our results show that in rheas, there are sexual differences in vigilance during both the breeding and the non-breeding seasons. During the non-breeding season, we did not observe males performing courtship displays. Therefore, although we cannot rule out that males in groups were more vigilant because they were competing for future mates, the hypothesis of male intragroup competition appears to be less likely.

There is no general pattern of sexual differences in vigilance in birds. Females are more vigilant than males in house sparrows and chaffinches (BEVERIDGE & DEAG 1987) and in white-breasted nuthatches (WAITE 1987), but the opposite trend is observed in willow tits (HOGSTAD 1988) and ostriches (BERTRAM 1980; BURGER &

GOCHFELD 1988). As in rheas, these sex-related differences in vigilance have no evident explanation.

Both males and females were more vigilant during the breeding season. One interpretation of this result is that food is more abundant at this time and therefore birds would need less time to fulfil their energetic requirements. Alternatively, the higher vigilance during the breeding season could be the result of a more intense sexual competition both in males and in females.

As regards how vigilance is increased, we found that sexual and seasonal differences in vigilance were the result of different processes. Sexual differences were the consequence of males raising their head more frequently than females (i.e. they have shorter feeding bouts) but there were no sex differences in the length of the intervals with the head up. This result differs from that found in ostriches (BERTRAM 1980), where sex differences in vigilance were the consequence of males having longer bouts with the head up. On the contrary, seasonal differences in vigilance were the result of males and females having longer vigilance bouts during the breeding season but there were no seasonal differences in the length of the feeding bouts.

Group Size Effect on Vigilance

During the non-breeding season, rheas were more vigilant when they foraged alone than when they did so in groups. These results are partially consistent with those reported by MARTELLA et al. (1995). These authors found a negative correlation between group size and vigilance for group sizes ranging from 1 to 11 birds. We also observed differences in vigilance associated with group size, but these differences were only between solitary birds and birds foraging in groups. In solitary birds, the higher level of vigilance was the consequence of longer vigilance and shorter feeding bouts. One confounding variable is that most solitary birds (9/10) were males and males have shorter feeding bouts than females. Thus, the differences in the length of the feeding bouts could be the result of sexual differences instead of group size differences. If this were the case, the main group size effect would be the increase in the length of the vigilance bouts for solitary birds. This process is the same as the one responsible for seasonal differences in vigilance. In contrast, the decrease in vigilance in larger groups of ostriches was the result of an increase in the length of the feeding bouts (BERTRAM 1980).

During the breeding season, there was a weak effect of group size on vigilance. This effect was due exclusively to the differences in vigilance between females foraging alone or in groups of two and females foraging in larger groups. However, our sample size for solitary females and females in groups of two is too small to strongly support a group size effect in females during the breeding season. As regards males, there was no difference in vigilance between solitary males and males foraging in groups. The increase in vigilance by males in groups could be the result of male–male competition for females as LOMBARDI (1994) suggested.

An alternative hypothesis for explaining the higher vigilance of solitary birds is that increased alertness might result from animals looking for conspecifics rather than predators (KREBS 1974). If solitary birds were looking for conspecifics to join them, it

would be expected that they also spent more time walking than birds in groups. However, we did not observe any difference in the proportion of time allocated to walking between birds foraging alone or in groups. Because of the higher proportion of time spent in vigilance, solitary birds foraged significantly less time than birds in groups. Hence, unless they were using richer patches, it would be expected that their intake rate was lower than that of birds foraging in groups. Food density appears to be homogeneous in our study area and some of the observations of birds foraging alone and in groups were made at the same place. Therefore it is likely that intake rate in solitary birds was lower than in birds foraging in groups. It is important to point out that solitary birds were generally males. A possible interpretation for this distribution would be that some males could have been choosing to forage alone to avoid competition with other males, or that they were being excluded from larger groups by dominant males.

Acknowledgements

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