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## Adjacent nesting and egg stealing between males of the Greater Rhea *Rhea americana*

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In a three year field study on a population of 350 Greater Rheas *Rhea americana* we followed the fates of 138 nests. In four of these nests we observed that, instead of one, there were two males sitting. These males were less than one metre apart and during the incubation period, they stole eggs from each other. There were no signs of aggression between them. The total number of eggs in these adjacent or double nests was similar to that in single nests. Each double nest began as a single nest but during incubation, a second male sat beside the first male and started stealing eggs. We discuss possible functional and mechanistic explanations of this apparently misdirected behaviour.

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The breeding behaviour of the Greater Rhea *Rhea americana* is unusual for birds, with the males assuming the full incubation of the eggs and the rearing of the young. In addition, the mating system of this species combines female-defence polygyny and sequential polyandry (Bruning 1974, Oring 1982, Handford and Mares 1985).

At the beginning of the breeding season there are aggressive encounters between adult males and a dominance hierarchy is established. The dominant male monopolises a harem of 3 to 10 females by excluding the other males. He builds a nest (a depression in the ground between 15 and 30 cm deep and 1 to 1.5 m in diameter) and displays to, and copulates with, all the females of his harem. They lay eggs communally in this nest at 2 to 3 day intervals for 7 to 15 days. The females deposit the eggs beside the male who rolls them into the nest with his bill. After laying eggs for one male, the harem may move on to lay eggs for a second male (Muñiz 1885, Bruning 1974, Martella et al. 1994). The male incubates the eggs for 37 to 45 days and during this time he only leaves the nest a few minutes per day. The eggs hatch synchronously and the chicks are precocial. The male remains associated with his chicks until the start of the next breeding season.

Individual distance between rheas, in particular when they are resting, is maintained throughout the year. When an intruder approaches a resting bird within 5 to 10 m, it responds with intention movements of biting (head-forward threat display, Raikow 1968). If the resting bird is sub-dominant to the approaching bird, it moves away slowly; otherwise it remains stationary and threatens the intruder (Bruning 1974). Incubating males are particularly aggressive and threaten and chase other rheas that approach their nest. This aggressive behaviour is even displayed towards the females of a male's own harem (Bruning 1974).

In this paper we report the occurrence, in natural conditions, of four cases of bizarre nesting behaviour for this species. In these events, a pair of males nested at a distance less than one metre apart without any signs of aggression, and during the incubation they stole eggs from each other.

### Study area and methods

The study was carried out in the province of Buenos

Aires, Argentina (36°25'S, 56°56'W) during the breeding seasons (October–February) of 1992–1993, 1993–1994 and 1994–1995. In our study site there was a population of approximately 350 Greater Rheas (55% males and 45% females) distributed in an area of 45 km<sup>2</sup>.

We searched intensively for nests all over the study site and found a total of 138 nests, 41 in the first breeding season, 58 in the second and 39 in the third. We followed their fates until the eggs hatched or the nests failed.

The eggs were individually numbered with water proof ink. At each visit we made a rough sketch of the position of the eggs relative to one another. Nests were visited between 10 am and 4 pm and the visits lasted less than 20 min. Normally, the male resumed incubation between 5 and 30 min after we had left the nest. Visits were kept as brief and infrequent as possible because disturbed rheas tend to abandon the nest.

Results are mean  $\pm$  standard error of the mean.

## Results

In four of the nests found, three in 1992 and one in 1994, we observed that there were two males sitting. These males were at a distance of less than one metre from each other. We call these nests with two males, adjacent or double nests. In our study site the distance between nests, other than the double nests, was between 100 and 1000 m.

In three of the double nests the two males were sitting when the nests were found. In each of these cases, one of the nests (nest A) seemed older than the other (nest B). Nest B still had patches of green grass in its base when it was found. In the fourth case there was only one male until day 30 of incubation, when a second male sat beside him and started stealing his eggs. In all four cases the double nests were found after laying had been completed.

In three double nests we found eggs to have been moved from nest A to B and vice versa. The position that the moved eggs adopted in the new nest was random (sometimes at the periphery, sometimes in the centre). In the fourth double nest the eggs were always in nest A.

During 20 visits to these four double nests we never observed any aggressive display between the incubating males. Because birds were not marked, switches of the incubating males between the adjacent nests cannot be ruled out.

The total number of eggs in the double nests (nest A + nest B) was  $27.75 \pm 3.63$  (range 21–35,  $n=4$ ) while the number of eggs in single nests was  $25.6 \pm 1.11$  (range 8–52,  $n=68$ ). Nest desertion in double nests was 50% (2/4) whereas in single nests it was 72.6% (98/134). There was no difference in nest desertion between single and double nests (Fisher exact test  $P=0.31$ ). Egg losses during incubation in the two successful double nests were 27.3% and 0% while egg losses during incubation in

Table 1. Sequence of events in one of the double nests (case 2). The numbers in brackets correspond to the eggs that were in the other nest in the previous visit.

| Date   | Nest A  | Nest B  | Total             |
|--------|---------|---------|-------------------|
| 9 Dec  | 25      | 10      | 35                |
| 11 Dec | 17 (1)  | 18 (9)  | 35                |
| 19 Dec | 13 (5)  | 18 (7)  | 33 <sup>(a)</sup> |
| 20 Dec | 0       | 30 (13) | 32 <sup>(b)</sup> |
| 28 Dec | 17 (17) | 13      | 30 <sup>(c)</sup> |

<sup>a</sup>Two eggs that were in nest B at the previous visit disappeared and 2 eggs were moved between nests A and B. <sup>b</sup>One egg from nest B disappeared and 2 eggs were moved between nests A and B. <sup>c</sup>Two eggs from nest B disappeared.

single nests were  $13.42 \pm 3.56\%$  (range 0–81.5%,  $n=35$ ). Hatching success in the two successful double nests was 87.5% and 71.4% whereas in single nests it was  $66.1 \pm 3.34\%$  (range 14.8–100%,  $n=34$ ).

The case history of the four double nests was as follows:

**Case 1:** This nest was found on 7 December 1992 with 25 eggs in nest A and 8 eggs in nest B. The distance between the borders of nests A and B was 50 cm. At all the following 6 visits we registered that eggs had been moved between nests. Nest A always had more eggs than nest B. During incubation 22 eggs were lost. On 8 January 1993 the double nest had been abandoned and 8 eggs and eggshell fragments remained.

**Case 2:** This nest was found on 9 December 1992 with 25 eggs in nest A and 10 eggs in nest B. The distance between the borders of the nests was 30 cm. At the following 5 visits eggs had been moved between nests. The number of eggs in nest A decreased from 25 to 0 and then increased to 17 whereas in nest B it increased from 10 to 30 and then decreased to 13 (Table 1 and Fig. 1A and 1B). On 4 January 1993 the double nest had been abandoned as a consequence of predation by hairy armadillos *Chaetophractus villosus*.

**Case 3:** This nest was found on 28 December 1992 with 21 eggs in nest A and no eggs in nest B. The distance between the borders of the nests was 90 cm. At the following 7 visits all the eggs were in nest A and nest B had no eggs. However, one male was always sitting in nest B (Fig. 1C). During incubation nest A lost 5 eggs. On 19 January 1993, 14 chicks hatched. After hatching, both males shared the care of the chicks.

**Case 4:** This nest was found on 8 December 1994. Until 15 December there was only one male incubating 22 eggs (nest A). Between 15 and 22 December a second male sat beside the first male. On 22 December there were 16 eggs in nest A and 5 in nest B. The distance between the borders of the nests was 30 cm. On 26 December, 15 chicks hatched. After hatching, both males shared the care of the chicks.

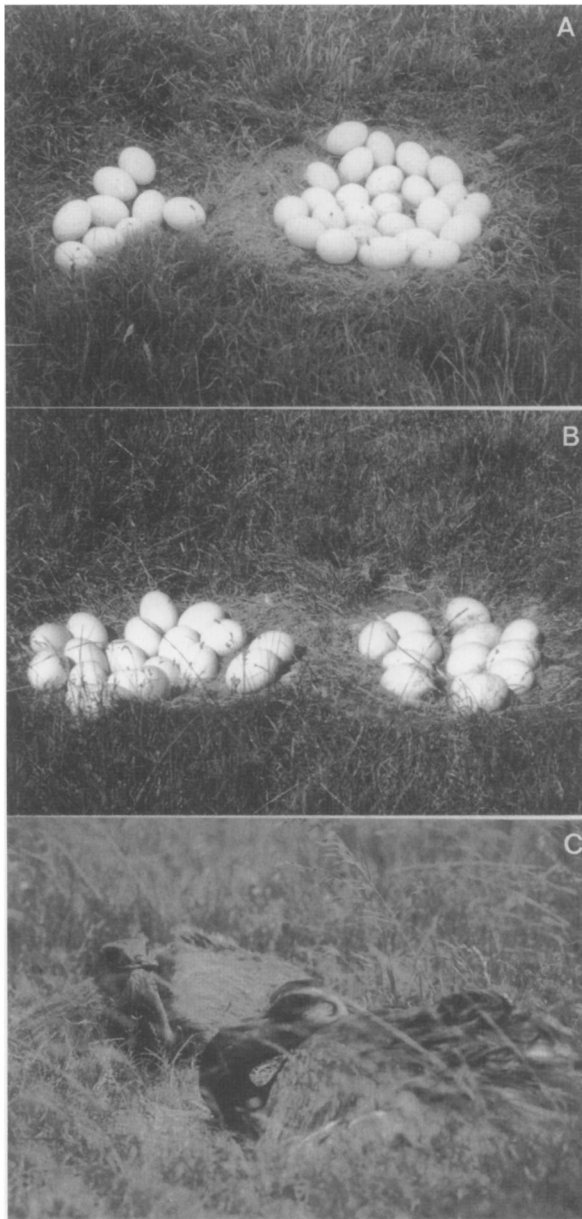


Fig. 1. Photographs A and B show two stages in one of the double nests (case 2). In photo A it is possible to observe that the nest on the right (nest A) seems older than the nest on the left (nest B). Photo B shows the same double nest ten days later. Photograph C shows two males sitting at another double nest (case 3).

## Discussion

These cases of adjacent nesting and egg stealing raise the question of the possible costs and benefits of this behaviour to each male. Regardless of whether the males of the double nests shared paternity in the clutches, the advantage of spending time and energy incubating eggs which could be incubated by another male is unclear. The number of eggs in double nests was not different

from the number of eggs in single nests and so they could have been incubated by a single male. Thus, both males could have incubated alternately using the rest of their time for foraging. As mentioned above, incubation lasts between 37 and 45 days and during this time the male only abandons the nest a few minutes per day for foraging (generally rheas spend 80% of the daylight time foraging). Therefore, even if incubation were energetically cheap (i.e. incubation metabolic rate similar to field metabolic rate), these males could have used the incubation time for feeding.

Direct observation of one double nest (case 4) and indirect evidence from the other three indicate that the double nests started with only one incubating male and that a second male sat beside him some time during the incubation.

The first male could benefit from having another male beside him. This second male could provide protection for the nest during incubation or for the chicks after hatching. However, it is not clear what the benefits for the second male are. One possibility is that second males could enhance the probability of being chosen as a mate by females in subsequent years or that they could acquire nesting or parenting experience that will help them in future years as happens with some helpers at the nest (Emlen and Wrege 1989). Because birds were not marked, this hypothesis cannot be ruled out.

Another possible benefit for the second male could be obtaining copulations when females visit the nest for laying. Almost 90% of the eggs are laid during the first 10 days after the first egg is laid (Reboreda and Fernández 1994). Therefore, most of the opportunities for obtaining copulations would occur during this short time window. There would be no benefit for the second male in remaining associated with the nest after females finished egg laying. However, in the four double nests the second males remained associated with the nests either until eggs hatched or the nest failed.

The lack of information about relatedness among the adjacent males limits speculations about kin selection explanations. However, it is important to point out that because of the polygynous mating system, the coefficient of relatedness between sibs in rheas is on average lower than 0.5. Therefore, even if these double nests were more successful than single nests (there is no evidence for this), a rhea that helped a relative to incubate eggs which had not been fathered by himself would receive a very low indirect gain in fitness.

One mechanistic explanation of this behaviour could be that pairing of nests is an "odd" error due to motivational factors. A double nest could occur when two males are unable to exclude each other when they are competing for the same harem. These males could share copulations with the same females and therefore both could be highly motivated to incubate the eggs, in particular if the females lay them in only one place. This interpretation would explain why the adjacent males tolerated each other and why the number of eggs found in

double nests was similar to the number of eggs found in nests attended by one male. In support of this, in a few cases we observed that two males were associated with the same harem of females.

The stealing of eggs has also been reported in a species of colonial bird, the Thick-billed Murre *Uria lomvia* (Gaston et al. 1993) in which individuals occasionally steal eggs from a neighbour after the loss of their own eggs. In a similar way, a rhea's double nest could be the result of one male losing his nest and being unable to get a new harem of females. It is interesting that all cases of double nests occurred at the end of the breeding season, when the number of sexually active females had decreased.

Since rhea males have a strong drive to retrieve eggs which are close (1–2 m) to their nest (Bruning 1974, personal observations), the stealing of eggs between males of adjacent nests could occur as a by-product of this behaviour, perhaps during the short periods when the males leave the nest for foraging.

Although double nests occurred at a very low frequency, this value could be an underestimate because some nests were found after they had been deserted and other nests were deserted before the end of the laying period.

Fighting between two males for the possession of a nest has been previously reported for rheas in captivity in a situation where there was simultaneous polyandry (Brito 1949). There has been only one previous field study in rheas (Bruning 1974); in that study 64 nests were found in two breeding seasons (but most of them were not monitored) and there were no reports of double nests. Therefore, our observations constitute the first records of this behaviour in natural conditions. Further studies involving marked birds and paternity analysis are needed to evaluate possible adaptive explanations for this seemingly misdirected behaviour.

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