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Egg losses and nest desertion in Greater Rheas *Rhea americana*

GUSTAVO J. FERNÁNDEZ[1]* & JUAN C. REBOREDA[1,2]
[1]*Institute of Biology and Experimental Medicine CONICET, Vuelta de Obligado 2490, 1428 Buenos Aires, Argentina*
[2]*Department of Biological Science, Faculty of Science Exactas and Natural, University of Buenos Aires, Pabellón II Ciudad Universitaria, 1428 Buenos Aires, Argentina*

Avian nest desertion should occur when the cost of attending the nest results in a reduction of parental fitness. In Greater Rheas *Rhea americana*, the male incubates the eggs so that the decision to desert the nest is made exclusively by him. Because of constraints, the timing of desertion may affect the possibility of renesting. We estimated nest desertion rates through the breeding season and at different stages of the nesting cycle (laying and early, mid- and late incubation). We also analysed the effect of egg losses at different stages of the nesting cycle on the probability of deserting the nest. Nest desertion rates decline throughout the breeding season. The probability of deserting the nest was higher during the laying stage and decreased through incubation. For all stages, egg losses were higher in nests that were deserted than in nests that were still active at the end of the corresponding stage. Egg losses were less likely to elicit nest desertion as incubation advanced. Egg losses in experimental (unattended) nests were not random. We postulate that egg losses during the first stages of the nesting cycle would be a good predictor of future egg losses and risk of nest failure. As females remain associated with the male during egg-laying and because incubation in rheas is an energetically costly activity that may affect renesting attempts, early nest desertion could increase a male's ability to remate and renest.

Breeding individuals should adjust their behaviour to maximize their expected lifetime reproductive success (Williams 1966). If parental decisions are based on the costs and benefits of parental care, avian nest desertion should occur when the cost of attending the nest results in a reduction of parental fitness (Clutton-Brock 1991). In avian species, most desertions occur during the clutch stage (Ricklefs 1969, 1977). Factors that cause clutch desertion include extreme weather conditions (Boersma 1976), lack of food (Anderson 1989), ectoparasite infestation (Duffy 1983), low quality of the parents (Wiggins *et al.* 1994, Yorio & Boersma 1994) and partial clutch loss (Armstrong & Robertson 1988, ten Cate & Taborsky 1992).

The use of past investment as the basis of parental care decisions has been the subject of extensive debate. Trivers (1972) proposed that, in order to minimize wastage of reproductive effort, parents should adjust their current expenditure to past investment. Several authors pointed out that current parental expenditure should be based on prospective benefits and not on past investment (Dawkins & Carlisle 1976, Boucher 1977, Maynard Smith 1977) and that organisms that use past investment in their parental investment decisions are committing an error of judgement (the so-called Concorde fallacy, Dawkins & Carlisle 1976). However, it is misleading to consider that animals that take into account past investment for their present investment decisions are committing the Concorde fallacy. Animals with fixed resources available for reproduction may use past investment as an accurate indication of resources available for reproduction (Dawkins & Carlisle 1976, Fagerström 1982, Coleman & Gross 1991). Accordingly, Coleman and Gross (1991) emphasized the importance of incorporating life-history theory in parental investment theory. The cost of reproduction results in a trade-off between present and future investment and therefore any changes in present investment must affect the ability

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*Corresponding author.
Email: mermoz@dna.uba.ar

to invest in the future.

In Greater Rheas *Rhea americana*, the decision to continue the incubation or to abandon the nest is made exclusively by the male. In this species the male undertakes the full incubation of the eggs and the rearing of the chicks. Dominant males monopolize harems of females that lay eggs communally in their nests (Muñiz 1885, Hudson 1920, Bruning 1974). Clutch size depends on harem size and varies from eight to more than 50 eggs (Fernández & Reboreda 1998). Incubation is from 36 to 45 days and during this time the male rarely leaves the nest (Bruning 1974, Fernández & Reboreda pers. obs.). However, in this species, more than 65% of the nests are abandoned and egg losses during incubation appear to be a cause of nest desertion (Fernández & Reboreda 1998).

The decision to desert the clutch is particularly critical for species with limited breeding opportunities. Incubating Greater Rhea males, like other ratites (Coddington & Cockburn 1995), must suffer a significant reduction in their fat reserves as a result of the long incubation period. Because of energetic and temporal constraints, the time at which the decision to desert the clutch is made may affect the possibility of subsequent breeding attempts. We estimated nest desertion rates at different times of the breeding season and stages of the nesting cycle. We also analysed the effect of egg losses at different stages of the nesting cycle on the probability of deserting the nest.

STUDY AREA AND METHODS

The study was conducted in three cattle ranches of approximately 3500, 800 and 2000 ha, situated near the town of General Lavalle in the province of Buenos Aires, Argentina (36°25′S, 56°56′W). The first two ranches (sites A and B) are contiguous whereas the third one (site C) is about 10 km from the others. The area is flat, low and marshy, with little of the land rising more than 10 metres above sea level. The native vegetation is of short grasses with scattered patches of woodland in the higher areas (for a detailed description of the study area see Fernández & Reboreda 1998). The number of rheas in sites A, B and C were approximately 250, 150 and 100, respectively. We estimated population size in our study sites by total counts performed each year at the end of the breeding and non-breeding seasons. Sex ratio was slightly biased towards males (55% males and 45% females).

Greater Rhea nesting attempts occur from September to December, although most of them are in November (Fernández & Reboreda 1998). During each breeding season we searched intensively for nests and found a total of 170 nests, 41 in 1992–93, 58 in 1993–94, 39 in 1994–95 and 32 in 1995–96. In total, 64 nests were found after the incubating male had deserted. Two of these nests started in September, seven in October, 18 in November and seven in December. For the remaining 30 nests, we were unable to determine the date at which they started. These 64 nests were excluded from our analysis because we were unable to determine the number of eggs lost before desertion and the stage of the nesting cycle at which desertion had occurred. We also excluded five nests found after the chicks had hatched, one nest that was visited only once, one nest destroyed by cattle and six nests predated by Hairy Armadillos *Chaetophractus villosus*. In the nests destroyed by cattle or predated by hairy armadillos, desertion was compulsory as the male could not continue incubation. Hairy Armadillos burrow a system of galleries that converge at the base of the nest and from which they steal eggs. The nest is usually destroyed (literally it sinks) and the male deserts. Therefore, we used for our analysis 93 nests that were found active at different stages of the nesting cycle (mainly egg-laying and early incubation) during the 1992–95 breeding seasons. Of these 93 nests, 51 hatched chicks.

In each nest, the eggs were individually numbered with waterproof ink, measured with callipers and weighed. Nests were visited between 09:00 and 17:00 h and visits lasted less than 20 min. At each visit, we determined egg losses and whether the male had deserted the nest, continued the incubation or the chicks had hatched. Generally, the male resumed incubation between 5 and 30 min after we had left the nest. Visits were kept as brief and infrequent as possible in order to minimize the risk of investigator-induced desertion. We have no evidence that our disturbance could have affected nesting success. We determined the date at which laying started either directly (we knew the date of laying of the first egg) or indirectly by backdating (the start of the laying was estimated as date of hatching minus 40 days) or by the colour of the eggs (they are light yellow when laid but become white in approximately five days). We use the term clutch size to refer to the number of eggs laid in the nest. As these eggs are laid by several females, the term clutch size is used for the total in the nest.

We used Mayfield's (1975) method to calculate daily nest mortality rates (as an index of nest desertion). Because this method uses only information from the period during which a nest was under observation, it avoids bias introduced by finding nests at different stages of the nesting cycle. Daily nest mortality rates (DNMR) were estimated by dividing the number of nests that failed by the total number of days the nests were under observation. The probability of survival for one day $\hat{s}$ was equal to 1 – DNMR. As intervals between nest visits were variable, we used the Johnson (1979) correction for estimating nest abandonment date. We estimated the variance (V) of $\hat{s}$ from Johnson's (1979) equation $V = [(\mathrm{ND} - \mathrm{losses}) \times \mathrm{losses}] / \mathrm{ND}^3$, where ND is the number of nest-days of exposure and losses the number of nests that failed (Mayfield 1975). We compared stage-specific mortality by using the statistic $\hat{s}_2 - \hat{s}_1 / [V(\hat{s}_1) + V(\hat{s}_2)]^{1/2}$, where the subscript specifies each nesting stage or period. If Johnson's statistic $> Z_{0.025}$ then the null hypothesis that the stages' survival probabilities were equal was rejected (Johnson 1979).

To evaluate whether there was any seasonal effect on DNMR, we divided the breeding season into periods of 15 days each. Because of the small number of nests at the beginning and end of the breeding season (one nest in September, five nests in October and six nests in February) and the inability to estimate DNMR with small sample sizes (Johnson 1979), we only considered nests from November to January.

We estimated DNMR for the following stages of the nesting cycle: laying (days 1–10), early incubation (days 11–20), mid-incubation (days 21–30) and late-incubation (days 31–40). Nests that were deserted or hatched chicks after day 40 were included in the last stage. For each stage, we determined the maximum number of eggs in the nest, the number of eggs lost and the percentage of the eggs lost during the stage. We compared these values between deserted and active nests. We considered as active those nests that were still active at the end of the corresponding stage. There were no significant differences in DNMR values between years for any nesting stage. We therefore pooled data from the 1992–95 breeding seasons.

To evaluate whether egg losses produced by partial predation were random, we used 20 natural nests that had been deserted during the breeding season. In each nest we placed seven to 20 Greater Rhea eggs and registered egg losses during the following 15–70 days. Nests were checked at intervals 1–5 days long. This design corrects for biases caused by male nesting activity (i.e. accidental breakage of eggs). Egg losses in these experimental nests were corrected by exposure time. We estimated egg losses for a 40-day period and compared them with those expected from a Poisson distribution. All significance levels are for two-tailed tests.

RESULTS

Time of the breeding season

DNMR declined throughout the breeding season (Spearman rank correlation, $Z = -2.11$, $n = 6$, $P < 0.05$, $\rho = -0.94$). It was negatively correlated with the number of nests in late incubation (Spearman rank correlation, $Z = -2.11$, $n = 6$, $P < 0.05$, $\rho = -0.94$) and there was a non-significant tendency towards a positive correlation between DNMR and the number of nests in the laying stage (Spearman rank correlation, $Z = 1.78$, $n = 6$, $P = 0.07$, $\rho = 0.79$, Fig. 1).

Stage of the nesting cycle

DNMR was significantly higher during laying and decreased progressively through incubation (Fig. 2). During our study, a high proportion of nests (64/170) was found after the incubating male had deserted (see Methods).

In these nests, clutch size was significantly smaller than in nests that were found while active and in which laying had been completed (mean ± se, 9.74 ± 1.17, $n = 62$ vs. 25.84 ± 1.01, $n = 80$; t-test, $t = 10.47$, df = 140, $P < 0.001$). This result would indicate that most of these nests were deserted before laying was completed.

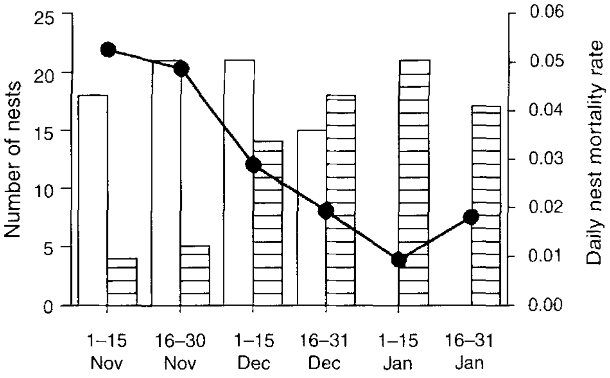

Figure 1. Number of nests that were in laying (days 1–10, unshaded bars) and completing incubation (days 26–40, hatched bars) during each period. ●, Daily nest mortality rates at different times of the breeding season. The number of nests under observation and failed for each period were, respectively: 16 and six (1–15 Nov), 33 and 11 (16–30 Nov), 36 and 10 (1–15 Dec), 37 and seven (16–31 Dec), 31 and three (1–15 Jan) and 17 and three (16–31 Jan). The total number of days all nests were under observation were: 120 (1–15 Nov), 237 (16–30 Nov), 356 (1–15 Dec), 369 (16–31 Dec), 324 (1–15 Jan) and 170 (16–31 Jan).

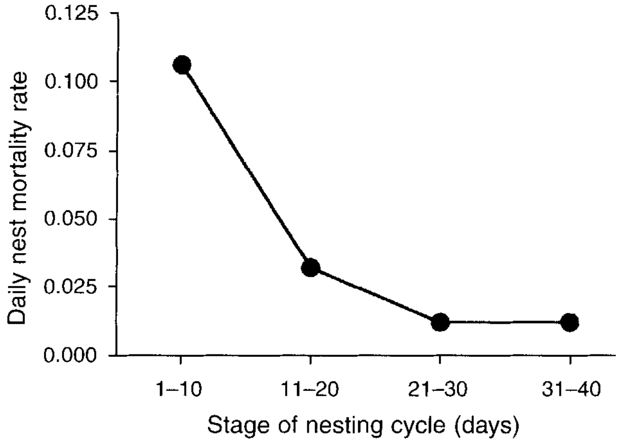

Figure 2. Daily nest mortality rates (●) at different stages of the nesting cycle. The number of nests under observation and failed for each stage were, respectively: 36 and 17 (days 1–10), 56 and 11 (days 11–20), 59 and six (days 21–30) and 59 and eight (days 31–40). The total numbers of days all nests were under observation were: 177.4 (days 1–10), 350.4 (days 11–20), 499.2 (days 21–30) and 686.8 (days 31–40). There were significant differences in DNMR between the following stages: days 31–40 vs. days 1–10, $P < 0.001$; days 31–40 vs. days 11–20, $P < 0.05$; days 21–30 vs. days 1–10, $P < 0.001$ and days 11–20 vs. days 1–10, $P < 0.01$.

Egg losses

Except for the laying stage (days 1–10), there were no differences in the maximum number of eggs in deserted and active nests (Mann–Whitney $U = -4.55$, $P < 0.001$ for days 1–10, $U = -0.32$, ns for days 11–20, $U = -0.36$, ns for days 21–30 and $U = -1.60$, ns for days 31–40, Fig. 3a). The number of eggs lost was higher in deserted than in active nests (Mann–Whitney $U = -3.09$, $P < 0.01$ for days 1–10, $U = -3.95$, $P < 0.001$ for days 11–20, $U = -1.21$, ns for days 21–30 and $U = -4.9$, $P < 0.001$ for days 31–40, Fig. 3b). The same pattern was found when we analysed the percentage of eggs lost in deserted and active nests (Mann–Whitney $U = -3.3$, $P < 0.01$ for days 1–10, $U = -3.98$, $P < 0.001$ for days 11–20, $U = -1.16$, ns for days 21–30 and $U = -5.07$, $P < 0.001$ for days 31–40, Fig. 3c). To evaluate whether males that had spent more time incubating the clutch had a higher threshold of egg losses before deserting the nest we compared the number and the percentage of eggs lost in nests that were deserted at different stages of the nesting cycle. Egg losses were significantly higher in nests deserted during days 31–40 than during any other stage (Kruskal–Wallis and contrasts for number of eggs $H = 21.58$, $P < 0.001$ and Kruskal–Wallis and contrasts for percentage of clutch lost $H = 28.3$, $P < 0.001$, Fig. 3b & 3c).

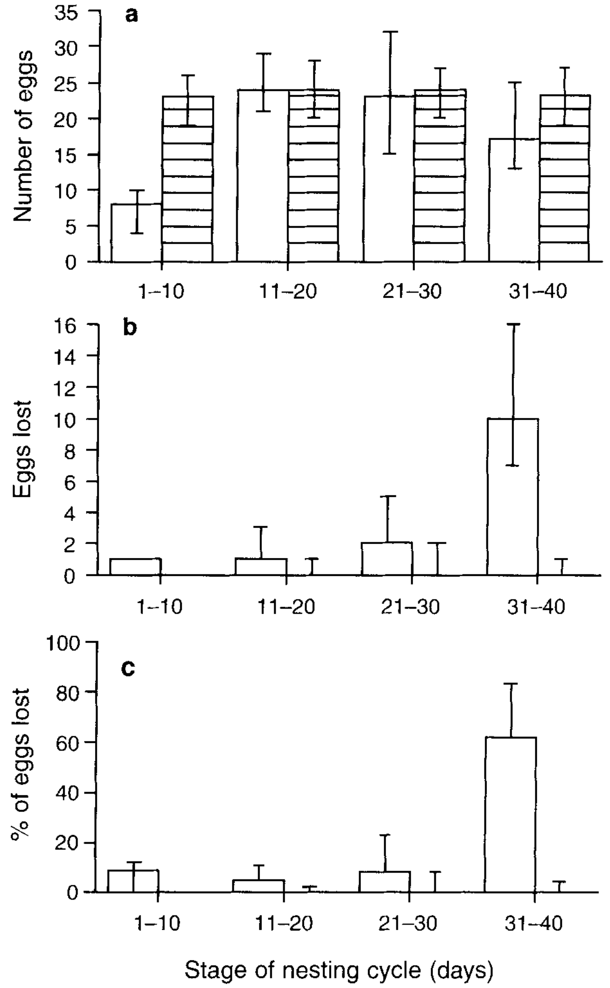

Figure 3. Medians and quartiles for the maximum number of eggs (a), the number of eggs lost (b) and the percentage of eggs lost (c) at different stages of the nesting cycle. Open bars, nests that were deserted; hatched bars, nests that were still active at the end of each stage. Note that all medians for the number and percentage of eggs lost in non-deserted nests are 0. The numbers of deserted and active nests for each stage were, respectively: 17 and 19 (days 1–10), 11 and 43 (days 11–20), six and 51 (days 21–30) and eight and 51 (days 31–40).

The rate of egg losses in the experimental unattended nests (see Methods) was 0.03 eggs/day. The pattern of egg losses was not random (Kolmogorov–Smirnov test, $D = 0.36$, $n = 20$, $P < 0.01$) as nests without egg losses or with many egg losses were more frequent than expected from a Poisson distribution.

DISCUSSION

Nest desertion in Greater Rheas declines throughout the breeding season and is more frequent during the early stages of the nesting cycle. The loss of eggs increases the probability of the male deserting the nest but males appear to be less sensitive to egg losses as incubation advances. These conclusions are supported by the following observations: (1) there was a seasonal decline in nest desertion that was negatively correlated with the number of nests completing incubation, (2) nest desertion was higher during laying and then decreased progressively through incubation, (3) egg losses were higher in deserted than in active nests and (4) egg losses were higher in nests deserted during late incubation than in nests deserted during any other stage. The pattern of egg losses observed in experimental unattended nests would indicate that egg losses are clustered in time and therefore Greater Rheas could use present egg losses as a predictor of future egg losses or risk of nest failure.

In other species with long incubation periods nest desertion occurs as a result of significant fat reduction in birds with poor body condition (Yorio & Boersma 1994). This explanation cannot account either for the higher desertion rates of rhea nests during the laying and early incubation (higher desertion rates would be expected during mid- to late incubation) or for the differences in egg losses between deserted and active nests.

In common with rheas, ostriches also have higher rates of nest desertion during the laying stage (Bertram 1992). Bertram attributed this difference to lower nest attendance during laying, a greater willingness to defend the nest during incubation and to differences in nest detectability (nests built in vulnerable sites are detected early during the nesting cycle). We found no differences in the time the incubating male spent at the nest during the nesting cycle (unpubl. data). We also have no evidence that nests deserted early were more detectable than others. Another difference between ostriches and rheas is that most cases of nest desertion in ostriches were the result of nest destruction (desertion was compulsory) whereas in Greater Rheas nest desertion was associated with the loss of a few eggs and therefore the male had the possibility of continuing incubation. Thus, the male's options in Greater Rheas were to continue investing in a reduced clutch, to abandon it and start a new one, or to abandon it and forego reproduction, saving reproductive effort for the next breeding season.

In rheas, most egg losses result from the breakage of infected eggs and partial predation, mostly by Hairy Armadillos, foxes and feral dogs (Fernández & Reboreda 1998). As mentioned above, rhea males are sensitive to the loss of eggs but the threshold increases as incubation advances. Our interpretation of this result is that the loss of eggs during the first stages of the nesting cycle would be a good predictor of future egg losses (either because the infections will spread to other eggs or because predators will tend to return to the same nest). Early nest desertion also could increase the male's probability of remating and renesting. During egg-laying the females remain associated with the nesting male, but once egg-laying has concluded they move on for mating with secondary males (Bruning 1974, Martella *et al.* 1994). Therefore, males deserting the nest after laying has ended must obtain a new harem. In addition, males that desert the nests at an advanced stage of the nesting cycle may have low energy reserves and therefore poor prospects of initiating a new nesting attempt. Thus, as incubation advances, the only benefit that could arise from deserting the nest is saving reproductive effort for the next breeding season.

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