EFFECTS OF CLUTCH SIZE AND TIMING OF BREEDING ON REPRODUCTIVE SUCCESS OF GREATER RHEAS

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ABSTRACT.—Greater Rheas (*Rhea americana*) have an unusual breeding system that combines harem-defense polygyny, communal egg laying, and exclusive male parental care. We studied survivorship of eggs and nests in relation to clutch size and timing of breeding and estimated the reproductive success of males and females. The number of eggs in a nest varied from 8 to 56, although in most cases it was between 20 and 30. Nests with more than 30 to 35 eggs had longer laying periods, lost more eggs during incubation, and had lower hatchability. As a result, the number of chicks hatched per nest increased with clutch size up to 30 to 35 eggs but decreased for larger clutches. More than 65% of the nests were deserted during incubation, and only 5 to 6% of the male population bred successfully each year. Nesting success was inversely correlated with rainfall during the breeding season and positively correlated with time of the breeding season. Chick survival during the first months after hatching averaged 60%. We suggest that the proportion of males that are able to attempt breeding is limited by energetic constraints. *Received 16 December 1996, accepted 21 August 1997.*

BIPARENTAL CARE is the norm in birds, occurring in more than 90% of the species (Lack 1968). In ratites and tinamous, however, incubation and brood rearing are performed predominantly or solely by males (Handford and Mares 1985). In the Greater Rhea (*Rhea americana*), males assume all of the incubation and chick-rearing duties. Rhea breeding activities begin with combat among adult males, and the dominant male excludes other males and monopolizes a harem of females that lay eggs communally in a single nest (Hudson 1872, Muñiz 1885, Bruning 1974). The male builds the nest and incubates the eggs for 36 to 45 days. During this time he rarely abandons the nest for feeding (Bruning 1974, Fernández and Reboreda pers. obs.). The eggs hatch synchronously and the chicks are precocial. The male leads the chicks to food and protects them during the first months after hatching (Bruning 1974, Fernández and Reboreda pers. obs.). After laying eggs for one male, some females move on to lay eggs for another male (Muñiz 1885, Bruning 1974, Martella et al. 1994). Thus,

the mating system combines female-defense polygyny and sequential polyandry (Oring 1982, Handford and Mares 1985). The extent to which polyandry occurs in wild populations of rheas is not well known. Bruning (1973) suggested that harem females may lay eggs for 10 to 12 different males in a season and that nests produced by later males generally are abandoned, thus producing a clear premium on dominant males that reproduce at the beginning of the breeding season.

Various hypotheses have been proposed to explain the evolution of communal nesting by females and uniparental care by males in ratites and tinamous. Clutton-Brock (1991) stated that if there is a positive relationship between clutch size and egg or chick survival, and if the size of clutches laid by individual females is constrained or egg or chick survival is affected by the interval between the start of laying and the onset of incubation, then nest sharing by females may evolve. Once several females lay eggs in a single nest, male care may be favored because each clutch represents a larger contribution to the male's fitness than to that of any single female, and the benefit/cost ratio of care may be higher for the male (Clutton-Brock 1991). In this scenario, females could desert their mates and produce clutches for other males. According to Trivers (1972), in species where uniparental care is sufficient for off-

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spring survival, if one sex shows some sort of territoriality or nest attachment, then selection will favor desertion by the other sex. Handford and Mares (1985) extended Trivers' ideas for explaining the evolution of male uniparental care and communal nesting in ratites and tinamous. They stated that, because these species have precocial young that require care from only one parent, and given environmental conditions that generate male territoriality, male uniparental care should evolve. If nest predation is a significant pressure, males should accumulate a clutch as rapidly as possible. If the reproductive output of females is best enhanced by laying additional eggs, then females should be serially polyandrous. In this scenario, the constraints on reproductive output of males would be the number of eggs they can cover and the time it takes to accumulate them, whereas for females, it would be the number of eggs they can lay and the number of males they can find.

Despite the importance of ratites and tinamous for understanding the evolution of mating systems and parental care, little information exists on the reproductive success of these species (but see Bruning 1974, Bertram 1992). Here, we present data on the survivorship of eggs and nests in relation to clutch size and timing of breeding and estimate the reproductive success of male and female Greater Rheas. Our intention is to present additional information on the breeding ecology of this species to promote the discussion and development of new hypotheses about the evolution of male parental care and female communal nesting in ratites and tinamous.

Study Area and Methods

The study was conducted near the town of General Lavalle (36°25′S, 56°56′W) in the province of Buenos Aires, Argentina, from June 1992 to April 1996. The area is flat, low (mostly <10 m elevation), and marshy. The native vegetation is composed of short-grass species with scattered patches of woodland in the higher areas. The study area is included in the so-called "flooding pampa" (Soriano 1991), one of the least-disturbed regions of pampa grasslands. This region is used almost exclusively for cattle grazing and still has a wild population of Greater Rheas.

Mean monthly temperatures in midsummer (January) are about 21°C, with absolute daily maxima between 35° and 38°C. In midwinter (July), mean monthly temperatures drop to about 7°C, with ab-

solute daily minima between -2° and -5°C. The average annual rainfall from 1981 to 1995 was 1,048 ± SE of 63 mm, and the annual rainfall during our study was 1,022, 1,420, 1,053, and 538 mm for 1992 through 1995, respectively. Normally, about 70% of the annual rainfall occurs during spring and fall.

The study was carried out in three cattle ranches of 3,500, 800, and 2,000 ha. The first two ranches (sites A and B) were contiguous, whereas the third (site C) was about 10 km from the others. Sites A, B, and C contained approximately 250, 150, and 100 rheas, respectively. The sex ratio was slightly biased toward males (55%). Natural predators of adult rheas (i.e. cougars [*Felis concolor*], and jaguars [*F. onca*]) have been extirpated from our study site. Rhea chicks suffer heavy predation from Crested Caracaras (*Caracara plancus*). Other potential predators of chicks are gray foxes (*Dusicyon gymnocercus*) and opossums (*Didelphis albiventris*).

During each breeding season (i.e. from September to January), we searched intensively for nests throughout the study site. Nests were found mainly by chance while driving slowly across the landscape. We found a total of 170 nests (41 in 1992, 58 in 1993, 39 in 1994, 32 in 1995). Sixty-four nests were found after the incubating male had deserted and five after the chicks had hatched. The other 101 nests were found during egg laying (44 cases) or after egg laying had ended (57 cases). We followed the fate of each nest until the eggs hatched or the nest failed. Four of the 170 nests (three in 1992 and one in 1994) were "double nests" (i.e. two males nested less than 1 m apart and during incubation stole eggs from each other; Fernández and Reboreda 1995). These double nests were excluded from analysis because the ways in which the males interacted may have affected nest attendance and hatching success.

In 140 of 170 nests, we determined the date of nest initiation either directly (we knew the date the first egg was laid) or indirectly by backdating (hatching date minus 40 days) or by the color of the eggs (light yellow when laid and white in ca. five days). In each nest, the eggs were individually numbered with waterproof ink, measured with calipers, and weighed (±10 g) using a 1-kg Pesola scale. Nests were visited between 0900 and 1700; visits lasted less than 20 min. Normally, the male resumed incubation within 5 to 30 min after we left the nest. Visits were as brief and infrequent as possible in order to minimize the risk of investigator-induced desertion. We have no evidence that our disturbance affected nesting success. After hatching, eggs that remained in the nest were dissected to assess the degree of embryonic development.

We use the term "clutch size" to refer to the total number of eggs laid in a nest. Because eggs are laid in the same nest by several females, our definition of clutch size is from the male's point of view. Nesting success was calculated as the number of nests at
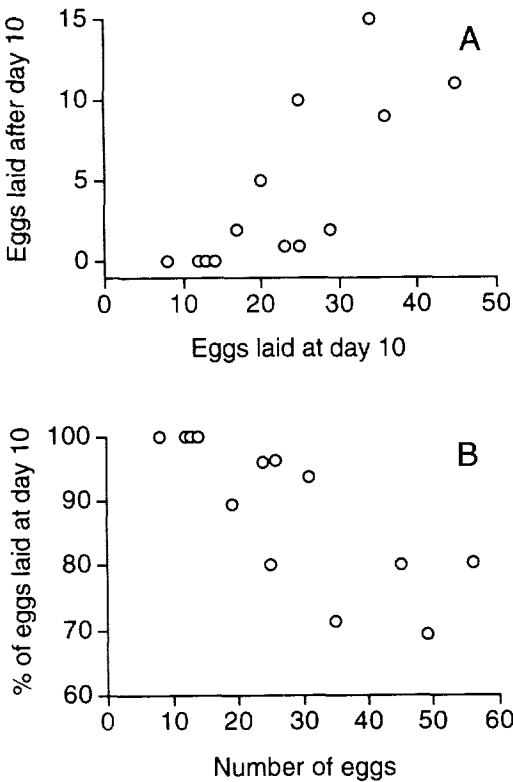
FIG. 1. (A) Number of eggs laid after day 10 as a function of number of eggs laid at day 10, and (B) percentage of eggs laid at day 10 as a function of total number of eggs laid. Data are for 14 successful nests found before day 5 of the laying period.
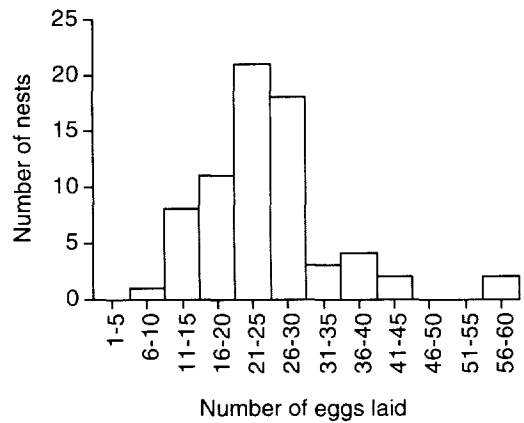

FIG. 2. Number of eggs laid at 70 nests in which laying was completed (45 nests that hatched chicks and 25 nests that were deserted after the end of the laying period).

cause they tend to resemble females. Data are presented as $\bar{x} \pm$ SE. Proportions were arcsine square-root transformed. All significance levels are for two-tailed tests.

RESULTS

Laying sequence, clutch size, and egg success.— The timing of laying was determined at 14 successful nests ($\bar{x} = 18.33 \pm 1.79$ eggs, range 8 to 56) that were found before day 5 of laying and that were checked four to eight times ($\bar{x} = 6.71 \pm 0.45$) before hatching. The percentage of eggs laid at days 5, 10, and 15 was 58.3 ± 5.8 (range 29 to 76.9), 89.4 ± 2.9 (range 69.4 to 100), and 95.8 ± 1.9 (range 80 to 100), respectively. The average number of eggs laid per day during the first 10 days was 2.31 ± 0.28 (range 0.8 to 4.5). Because female rheas lay eggs at intervals of two to four days, the number of eggs laid at a given time is an index of the number of females involved in egg laying. There was a positive association between the number of eggs laid at day 10 and the number of eggs laid after day 10 ($r^2 = 0.56$, $P = 0.001$; Fig. 1A), which indicates that nests with larger numbers of eggs had larger harem sizes. In addition, the percentage of eggs laid at day 10 was negatively correlated with clutch size ($r^2 = 0.7$, $P = 0.0002$; Fig. 1B), which indicates that the laying period increased with clutch size.

Nests contained between 8 and 56 eggs, although most nests had 20 to 30 eggs (Fig. 2). On average, the number of eggs in completed nests

which some eggs hatched divided by the number of nesting attempts during the breeding season, egg success was calculated as the number of eggs hatched divided by the total number of eggs laid in that nest, and hatchability was calculated as the number of eggs hatched per nest divided by the number of eggs in the nest immediately before hatching (number of eggs laid minus eggs lost during incubation).

At the end of the breeding season (i.e. February to April) each year, we estimated the number of adult birds and groups of males with chicks in sites A and B by direct counting with 12×50 binoculars while driving slowly through the area. Censuses were conducted in one day and following one direction to avoid counting birds twice. During 1995, we also conducted a census at the end of the nonbreeding season (i.e. August) to estimate the number of chicks that had survived after the winter. Sexes were distinguished by size and color of the plumage. Juveniles are easy to recognize by size until they are 10 months old but become difficult to distinguish thereafter be-
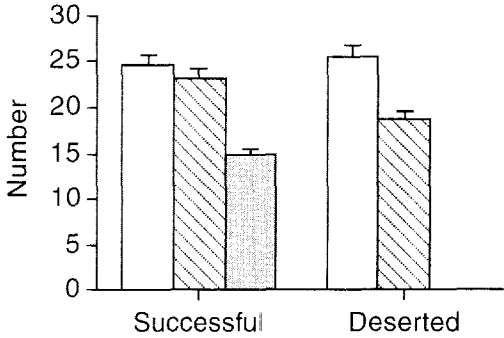
FIG. 3.   Number of eggs laid (open bars), number of eggs before hatching (hatched bars), and number of chicks hatched (shaded bar) in 45 successful and 25 deserted (after day 15) nests. For deserted nests, open and hatched bars correspond to number of eggs laid and number at time of nest desertion, respectively.

(45 successful nests and 25 nests deserted after the laying period) was 24.87 ± 1.06. The number of eggs laid per month varied among months (F = 3.92, df = 2 and 66, P = 0.025; September excluded), and nests started in November had higher clutch sizes than those started in December ($\bar{x}$ = 27.93 ± 2.0, n = 29 vs. $\bar{x}$ = 21.64 ± 1.13, n = 28; Scheffé's test, P = 0.025).

Most nests suffered egg losses during incubation as a result of predation or egg breakage. The total number of eggs laid did not differ between successful and deserted nests (t = 0.84, P = 0.69; Fig. 3), but the number of eggs in the nest before hatching in successful nests was significantly higher than that before desertion in deserted nests (23.11 ± 1.21 eggs vs. 18.68 ± 1.89 eggs; t = −2.06, df = 68, P = 0.043; Fig. 3).

On average, hatchability was 68.2 ± 2.8% (14.8 ± 0.63 chicks per nest, range 5 to 23, n = 45). Hatchability did not differ significantly among months (F = 0.19, df = 2 and 41, P = 0.83) or among years (F = 1.74, df = 3 and 41, P = 0.17). In 26.3 ± 5.2% of the 39 nests where we dissected unhatched eggs, the unhatched eggs showed no sign of embryonic development, in 35.9 ± 5.7% of the cases the eggs were rotten, and in the remaining cases the development of the embryos was incomplete. In 18.3 ± 4.2% of the cases, the embryo was at an intermediate stage of development, and in 19.5 ± 4.2% of the cases the development was almost complete (at six nests a chick hatched one to three days after the male had left the nest with the other chicks).

To assess whether clutch size affected egg survival, we performed a quadratic polynomial regression with number of eggs laid as the independent variable and number of eggs present before hatching as the dependent variable. There was a significant effect of the total clutch laid on the number of eggs before hatching (F = 561.1, df = 2 and 44, P < 0.0001). The number of eggs before hatching increased with number of eggs laid, but nests with larger clutches suffered higher egg losses than nests with smaller clutches (t = 11.2, P = 0.0001 for the linear term, and t = −3.7, P = 0.0006 for the quadratic term; Fig. 4A). Also, there was an effect of the number of eggs on hatchability (F = 12.4, df = 2 and 44, P = 0.0001). This effect was not significant for clutch sizes smaller than 30 eggs, but for larger clutches there was a significant negative effect (t = 0.89, P = 0.38 for the linear term, and t = −2.02, P = 0.05 for the quadratic term; Fig. 4B). As a result of the effects of clutch size on egg losses and hatchability, the number of chicks that hatched in a nest increased with the number of eggs laid up to 30 to 35 eggs, but then decreased (t = 6.39, P = 0.0001 for the linear term, and t = −6.06, P = 0.0001 for the quadratic term; Fig. 4C).

Nesting success.—We determined the fate of nests (deserted or successful) in 164 of 166 cases. Only 52 of these nests (31.7%) were successful. Nesting success varied significantly among years (G = 13.52, P = 0.004). The percentages of successful nests were 36.1 (13/36 nests), 24.1 (14/58 nests), 18.4 (7/38 nests), and 56.2 (18/32 nests) for 1992 through 1995, respectively. The main causes of nest desertion were rainfall, egg losses, and nest predation by hairy armadillos (*Chaetophractus villosus*). Nesting success tended to decrease with increasing rainfall during the breeding season (r^2 = 0.82, P = 0.09; Fig. 5).

Most nesting attempts occurred during the second half of the breeding season (considering the start of the breeding season as the date of the first nest attempt). On average, the percentage of nesting attempts during September and October was 2.2 and 15.9, whereas in November and December it was 47.1 and 34.8. Most nesting attempts during September and October were unsuccessful (Fig. 6). To evaluate if there was a seasonal effect on nesting success, we used a general linear model, with success of the nest as the dependent (binary) variable,
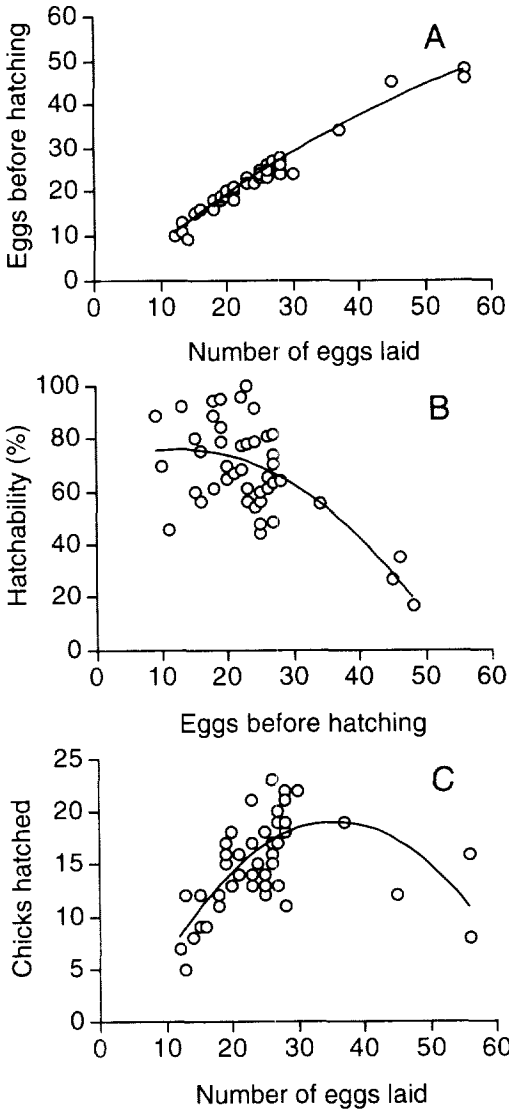
FIG. 4. (A) Number of eggs before hatching as a function of number of eggs laid, (B) hatchability as a function of the number of eggs before hatching, and (C) number of chicks hatched as a function of number of eggs laid; n = 45 successful nests.
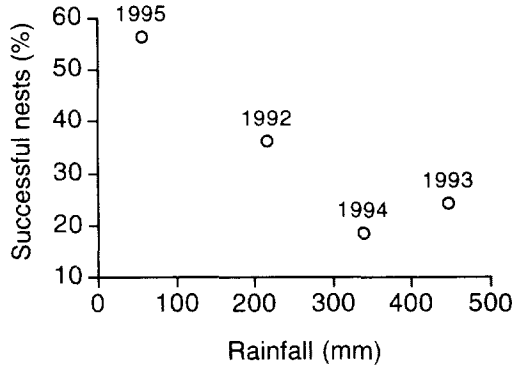

FIG. 5. Proportion of nests that hatched chicks as a function of rainfall during the breeding season; n = 164 nests (36, 58, 38, and 32 from 1992 to 1995) for which we determined fate.

date of the nesting attempt (measured as days elapsed since the first attempt) as the independent variable, and year as the categorical variable. The effect of date of nesting attempt on success of the nest was marginally significant (F = 3.17, df = 1 and 131, P = 0.077; Fig. 7), and the interaction between year and date of nesting attempt was not significant (F = 1.03, df = 3 and 131, P = 0.38). The temporal pattern of nesting attempts and nesting success differed among years. In particular, 1995 was characterized by a higher percentage of successful nests and by more early successful nesting attempts. When we repeated the previous analysis excluding the 1995 nests, the effect of date of nesting attempt became more significant (F = 7.11, df = 1 and 131, P = 0.009), whereas the interaction between year and date of nesting attempt remained nonsignificant (F = 0.197, df = 3 and 131, P = 0.82).

Chick survival.—At the end of the breeding season each year, we conducted censuses in sites A and B to determine the proportion of males with chicks and chick survival during the first months after hatching (Table 1). We found no evidences of dispersal of males with chicks from the study area during the first months after hatching. On average, the number of chicks per male was 8.89 ± 1.01 (range 2 to 33, n = 37 groups of males with chicks). Based on an average of 14.9 chicks hatched per nest, chick mortality during the first months after hatching averaged 40.2%.

Each year, only small proportions of males (4.5 to 6.1%) bred successfully and were accompanying chicks two to three months after hatching. At this time, the number of chicks as a percentage of the adult population was 25.6 ± 4.3% (range 16.8 to 37.4%). Generally, males remained associated with their chicks during the first four to six months after hatching, after which juveniles joined winter flocks. The proportion of juveniles during the August 1995 census (i.e. the end of the nonbreeding season)
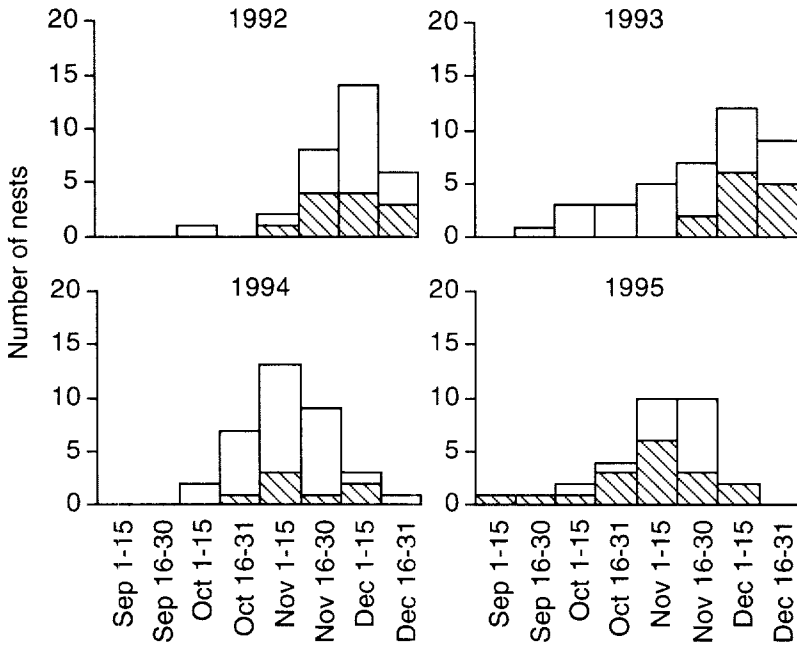
FIG. 6. Number of nesting attempts at different times of the breeding season, 1992 to 1995. The hatched portion of bars indicates the number of nests that hatched chicks; n = 136 nests that could be assigned to the 15-day periods.

was 24.5% (78/319), whereas the proportion of chicks in February 1995 was 26.1%. Thus, winter mortality in this population appears to be very low.
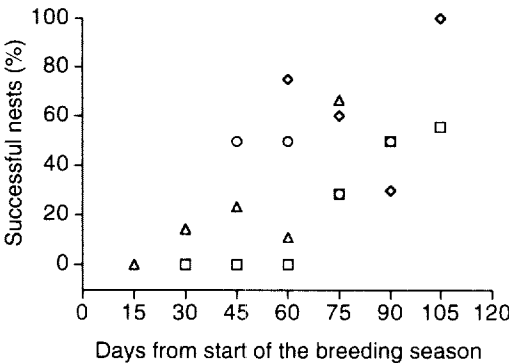

FIG. 7. Proportion of nests that hatched chicks (per 15-day interval) as a function of date of nesting attempt (days elapsed since first nesting attempt of the season). Periods for which there was only one nesting attempt are excluded. Circles, squares, triangles, and rhombuses correspond to nesting attempts during 1992, 1993, 1994, and 1995, respectively.

DISCUSSION

Laying sequence, clutch size, and egg success.— The laying patterns we observed indicate that the total number of eggs in a nest and the length of the laying period are affected by the number of females laying eggs at that nest. According to Guittin (1985), 80% of the eggs are laid at intervals of two to four days (39% of the eggs are laid at three-day intervals). In our study, the minimum and maximum numbers of eggs at day 10 were 8 and 45, respectively. Therefore, the minimum number of females laying for one male (assuming that each female lays at two-day intervals) would range from two to nine. These values are similar to those observed in reproductive groups (groups of one male and several females at which the male performs sexual displays; Fernández and Reboreda pers. obs.). The relationship between harem size and length of the laying period could result from females in larger harems: (1) laying for longer periods (each female laying more eggs or laying eggs less frequently), or (2) laying more asynchronously.

In most completed nests, clutch size varied

TABLE 1. Number of adult Greater Rheas, number of males with chicks, and number of chicks observed in censuses performed at the end of the breeding season, 1992 to 1995. The percentage of males that bred successfully was calculated assuming a ratio of 55 males to 45 females.

Year	No. adults	No. males with chicks	No. chicks	% Males with chicks[a]	No. chicks per male[b]	% Chicks[c]
1993	393	12	87	5.6	7.3 ± 1.5	22.1
1994	202	5	34	4.5	6.8 ± 1.2	16.8
1995	287	8	75	5.1	9.4 ± 1.3	26.1
1996	356	12	133	6.1	11.1 ± 2.5	37.4

[a] Percentage of males in the population that bred successfully.
[b] Number of chicks per male ($\bar{x}$ ± SE).
[c] Number of chicks as a percentage of the number of adults in the population.

from 20 to 30 eggs, and in only a few nests was it larger than 35 eggs. Nests with ≥35 eggs lost more eggs during incubation and had lower hatchability. The higher egg loss in these nests could have resulted from a higher proportion of eggs with bacterial infections (such eggs often explode during incubation). It is also possible that these nests had a higher rate of egg breakage due to males having difficulty rotating the eggs. The lower hatchability of eggs at these nests could have resulted from the high proportion of eggs that were laid long after incubation had begun. Male rheas start incubating two to three days after the first eggs are laid (Bruning 1974). Although rheas may attain hatching synchrony even though incubation begins before the entire clutch of eggs is laid (Bruning 1974, Cannon et al. 1986), it is likely that eggs laid 10 to 15 days after the onset of incubation have a lower probability of hatching. Hatchability probably also decreased because of lower incubation efficiency. We observed that it was difficult for incubating males to cover all of the eggs when clutches exceeded 30 eggs. Rotation of the eggs also was more difficult because some of the eggs became partially buried during incubation. In addition, rhea eggs weigh approximately 650 g, and a clutch of 40 to 50 eggs represents a mass of 26 to 32.5 kg. Male rheas weigh between 30 and 40 kg; thus, in nests with large clutches, males had to transfer heat to a total mass of eggs almost as large as their own mass.

On balance, large clutches were costly to both males and females. Males accepted all of the eggs that were laid in and close to their nests, even if these eggs were laid long after incubation had begun (males accepted eggs up to five days before hatching). These observations indicate that the number of eggs in a nest is de-

termined largely by the size of the harem. One possible reason why females lay eggs in nests with large clutches (or why they participate in large harems) is that there is a surplus of sexually receptive females. All nests with large clutches occurred during November, which was the peak month for nesting attempts. These nests contained more eggs, indicating that more females were laying eggs. On the contrary, at the end of the breeding season (December), we observed a decline in both the number of nests and the number of eggs per nest, indicating a decrease in the number of males ready to nest and in the number of females ready to lay eggs.

Nesting success and timing of nesting.—Rainfall could have affected nest desertion directly as a consequence of flooding, or indirectly by increasing the probability of nest predation by armadillos or other predators. Hairy armadillos create a gallery of burrows that converges at the base of the nest and from which they steal eggs. The nest is usually destroyed (literally, it sinks), and the male rhea deserts. In years of high rainfall, male rheas nest in the higher areas where armadillos are more abundant. In contrast, in years of low rainfall, males nest at places that normally are flooded and where armadillos are absent. These places also have higher cover such that nests are less easily detected by other nest predators.

Although reproductive success differed among years, it tended to increase as the season progressed. This result is interesting because reproductive success declines seasonally in most bird species (Perrins 1970, Daan et al. 1988). This decline is a consequence of differences in quality between early and late breeders, seasonal variation in the environment, or a combination of both (Hochachka 1990, Hatch-

well 1991, Ens et al. 1992, Nilsson 1994, Verhulst et al. 1995). For Greater Rheas, the seasonal increase in nesting success could have resulted from differences in quality between early and late breeders (e.g. late breeders with more fat reserves are less prone to nest desertion), or seasonal variation in the environment. However, in four breeding seasons we observed no correlation between rainfall and nesting success. Rainfall during the first (September to October) and second (November to December) half of the breeding season was 160 and 78 mm in 1992, 162 and 443 mm in 1993, 244 and 189 mm in 1994, and 44 and 41 mm in 1995. The higher nesting success of late breeders does not necessarily imply that they had higher reproductive success. Reproductive success of these males could have been diminished by other costs such as lower certainty of paternity or lower probability of survival to maturity of their chicks. Besides, early breeders could renest after nest failures, and early nesting attempts could be successful in some years (like in 1995), producing a premium on males that reproduce at the beginning of the breeding season. Thus, at present we have no clear explanation for the seasonal increase in nesting success and its correlation with male reproductive success.

Reproductive success of males and females.—In our study area, a population of approximately 500 birds attempted fewer than 45 nests per year. These values indicate that less than 20% of the males (assuming that each nesting attempt corresponded to a different male) try to reproduce during a breeding season. This low proportion of nesting males could have resulted from a low number of males that were physiologically ready to start a nest, or a low number of females that were ready to lay eggs during the breeding season. The former hypothesis could be related to the energetic costs of male parental care in Greater Rheas. In this species, males feed very little during the approximately 40-day incubation period (Bruning 1974, Fernández and Reboreda pers. obs.). After hatching, males remain associated with their chicks for three to six months, during which time they allocate more time to vigilance and less time to feeding than do solitary males or nonbreeding males or females in groups (Fernández and Reboreda pers. obs.). Therefore, it is likely that only those males that have enough fat reserves

at the beginning of the breeding season can afford to reproduce. If we take into account that a high proportion of nests is deserted, the emerging picture is that only 5 to 6% of the males breed successfully each year.

Concerning the reproductive success of females, as a consequence of nest desertion, egg loss during incubation, hatching failure, and chick mortality during the first months after hatching, approximately 10% of the eggs that were laid produced 3-month-old chicks. These eggs were laid in a few nests and therefore only a small proportion of the females bred successfully each year. Assuming an average harem size of five to six females and no sequential polyandry, we estimate that approximately 30% of the females breed successfully each year.

Because female Greater Rheas may lay eggs sequentially for 10 to 12 different males (Bruning 1973), most males should have an opportunity to breed sometime during the breeding season. However, our results show that only a small proportion of the males tries to reproduce each season. Consequently, unless only a few females in the population lay eggs during the breeding season, sequential polyandry in Greater Rheas is much lower than previously thought.

Abandonment and predation of nests are the most important factors that affect the reproductive success of Greater Rheas. The fact that some of the natural predators were absent at our study site suggests that the present rate of nest predation is lower than that experienced by Greater Rheas in the past. In Ostriches (*Struthio camelus*), the only other ratite for which data on nesting success are available, nest predation also is a very significant cause of reproductive failure (Bertram 1992). Harem size, clutch size, and synchrony of laying appear to be the other main factors affecting reproductive success of males and females. Unfortunately, data on egg success as a function of clutch size are not available for other ratites. Our data indicate that nest predation and synchrony of laying (and hatching) could have been significant pressures favoring the evolution of polygyny and communal nesting in Greater Rheas.

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