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MATING BEHAVIOR OF THE MALE GREATER RHEA

THAÏS L. CODENOTTI¹ AND FERNANDO ALVAREZ^{2,3}

ABSTRACT.—During mating, and during the phases known as solitary male, harem formation, and harem, male Greater Rheas (*Rhea americana*) became vigilant to assure the elimination of competitors. High rates of harem defense and male expulsion were observed at the start, with levels decreasing gradually through the phases of mating, and male-male fighting mainly limited to the phase of harem formation. Courtship was nonexistent early in the mating period, reached a high level during the phases of harem formation and harem, then declined markedly just before harem breaking. The rates of all male social activities decreased significantly just before harem breaking. Received 2 June 2000, accepted 17 January 2001.

Greater Rheas (*Rhea americana*) living in open grasslands of Argentina are typically polygynandric, i.e., the males are simultaneously polygynous, while the females are sequentially polyandrous (Bruning 1973, 1974; Handford and Mares 1985). In an agricultural area of Rio Grande do Sul, in southern Brazil, Greater Rheas occupy grassland and cultivated land, and exhibit their characteristic polygynandric mating system, without ever changing to monogamy, even when the sex ratio is near unity.

Greater Rheas in the present study area (Rio Grande do Sul) pass through three phases during mating: (A) Solitary male. From the middle of winter and through spring, mainly from August to November, adult males leave the mixed flocks, the latter including 4–35 animals of both sexes and all ages. The solitary males follow the mixed flock for approximately 25 d, at a distance of 30–300 m, usually keeping within sight of the mixed flock. (B) Harem formation. Also mainly from the middle of winter and through spring, the isolated males return to the mixed flocks where they stay for about one month, competing aggressively with other adult males, courting, and finally associating with a female subgroup. (C) Harem. Mainly during spring, the male with a subgroup of 2–12 females leaves the mixed flock to reside in a particular area for about 30–45 d, where nesting and joint laying take place (Codenotti 1995, 1997).

Bruning's (1974) field study of Greater

Rheas living in a grassy floodplain in the Buenos Aires province of Argentina was restricted to the middle of the breeding season (November and December 1970, and October and November 1972). Consequently he had to rely on reports from local residents for information on the early phases of mating. According to those reports and Bruning's observations, adult males were the first to leave the winter flocks as aggression increased early in the breeding season (this corresponds to our solitary male phase of mating). Contrary to our observations (Codenotti 1995, 1997), Bruning (1974) reported the formation of small female groups (2–15 members) which then became harems by the addition of an adult male. According to Bruning (1974), the primarily masculine behaviors of courtship and aggression occurred only and mostly, respectively, during the breeding season. At the onset of this period, and prior to acquiring a harem, males engaged in aggressive interactions and calling, and from that time the rate of courtship increased steadily.

In regard to Bruning's (1974) and Codenotti's (1995, 1997) reports, the mating process of Greater Rheas may be best understood by concentrating on the behavior of reproducing adult males. We approached that aim in the present study by analyzing the variation of the reproductive males' behaviors in relation to the phases of mating.

STUDY AREA AND METHODS

The 1680-ha study site was located at 28° 4' S, 52° 2' W in the northern portion of Rio Grande do Sul, Brazil, and was characterized by a humid subtropical climate. About 70% of the area was dedicated to farming, and most of the remainder was meadow (natural and cultivated). The Greater Rhea population in the study area varied during the period of study from about

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100–125 individuals, and the number of adult females per male was 2.1 in 1990, 1.4 in 1991, and 1.1 in 1992.

During a total of 82 weekly sampling journeys from January 1991 to December 1992 (14 such weekly journeys were skipped due to bad weather) a fixed route in the study area was followed, and the numbers of birds integrated into mixed flocks (made up of animals of both sexes and all ages) or harems, as well as solitary, were recorded. In addition, during a total of 127 sampling journeys during the mating season (August to February of 1990 to 1992, at 08:00–12:00 and 14:00–20:00 DST), 363 h of approximately equally distributed 15-min focal observations were made of the behaviors of the 16 breeding adult males that were individually recognized by differences in body size and plumage (Codenotti 1995). Rates of behaviors were then analyzed in relation to the three phases of mating and to the first and second halves of the duration of the harem phase for each male (Friedman two-way analysis of variance by ranks, Wilcoxon matched-pairs signed-ranks test, and sequential Bonferroni test; Siegel and Castellan 1988, Sokal and Rohlf 1995, with the aid of StatView 4.1 for Apple-Macintosh). The ranges of dates for the different phases of mating among the 16 subjects were: 20 July to 23 December for the solitary male phase, 25 July to 31 December for harem formation, and 6 September to 15 January for the harem phase.

The patterns of behavior were as follows (for more detail see Brito 1949; Raikow 1968, 1969; and Codenotti et al. 1995): (1) Comfort behavior—grooming and pecking at own feathers, shaking, opening wings, stretching, yawning, and also including neutral postures (standing, sitting, lying down). (2) Feeding—pecking the soil, vegetation, or insects (on ground or flying), and also including drinking. (3) Locomotion—walking and running. (4) Alert posture—motionless or walking slowly, with neck stretched up and head forward. In this posture, the bird moves head laterally, turning it to all directions. (5) Courtship—performed by male while walking within the group of females, or directed toward one particular female, often when trying to drive her to the harem. The male walks while opening his wings forward, lowering them, and dragging the tips on the ground, thus uncovering his body and showing his penis. Vertical and lateral swinging movements of the neck may be added. (6) Copulation—the female sitting down on her tarsi in front of the male, resting her abdomen on the ground. The male responds by sitting behind her (also resting on his tarsi), and while grasping the feathers on the back of her lower neck with his bill makes violent thrusting movements. (7) Booming call—hissing and purring, emitted by threatened subjects, and bill clapping by one animal chasing another (Codenotti et al. 1995). Adult males also emit booming calls during the reproductive season; there are no sounds specifically directed by males towards females. The booming call is produced by adult males while standing with stretched neck, the glittering black neck feathers becoming more conspicuous as the neck swells during the emission. The call

is a low-pitched, intense guttural sound made up of two syllables. Audio recording was done with a Sony digital recorder and a Sennheiser ME88 directional microphone with frequency range of 20–20,000 Hz, and the digital sonagram used was Uniscan II. Sonagram of booming call is presented in Codenotti et al. (1995). Only one sound, or a bout of two sounds with an interval of 2–3 s between emissions, are produced. Then the male remains silent for about 20 min before calling again. On several occasions we were able to detect the sound up to a distance of 3 km. While facing toward each other at close range, two males may call simultaneously in the context of competition for females, sometimes just before fighting or before starting a chase, but not during the actual fight or chase. Often the harem owner calls towards a male competitor 3–20 m away from him, the receiver being either visible or hidden by obstacles. There is some variation in the features of the calls of different males, and our observations suggest that stronger males tend to vocalize more often than others. (8) Harem defense—the harem owner, with wings open and flexed forward (thus exposing body and penis), facing another male at a distance of 3–20 m. He then moves to place himself between the intruder and his females, while trying to drive the harem away from the opponent. (9) Male-male fighting—often after calling, two adult males approaching and facing each other with neck and head feathers bristled and both wings (or seldom only one wing) raised. They then run toward each other. During the fight they hit each other with their feet and peck at each other while interlocking their necks. They may also chase each other while clattering the upper and lower jaws. (10) Male expulsion—as the result of a fight, the winner chasing the loser away from the area.

RESULTS

The monthly average number of birds included in the mixed flocks and harems, as well as that of solitary males is presented in Fig. 1. The breaking of the mixed flocks (from which solitary males, female groups, and harems originate) took place during winter and spring, with most of the harems disappearing by the middle of summer. The first nests were seen in September, and incubation extended until late December or January.

Significant differences among the average rates of behaviors of the 16 adult males during the three phases of mating (solitary male, harem formation, and harem) were found for all social activities (alert posture: $\chi_r^2 = 16.6$; courtship: $\chi_r^2 = 24.1$; calling: $\chi_r^2 = 18.4$; harem defense: $\chi_r^2 = 24.9$; male-male fighting: $\chi_r^2 = 15.7$; male expulsion: $\chi_r^2 = 19.1$; $df = 2$, $P < 0.001$; Friedman two-way analysis of variance test). Differences in comfort behav-

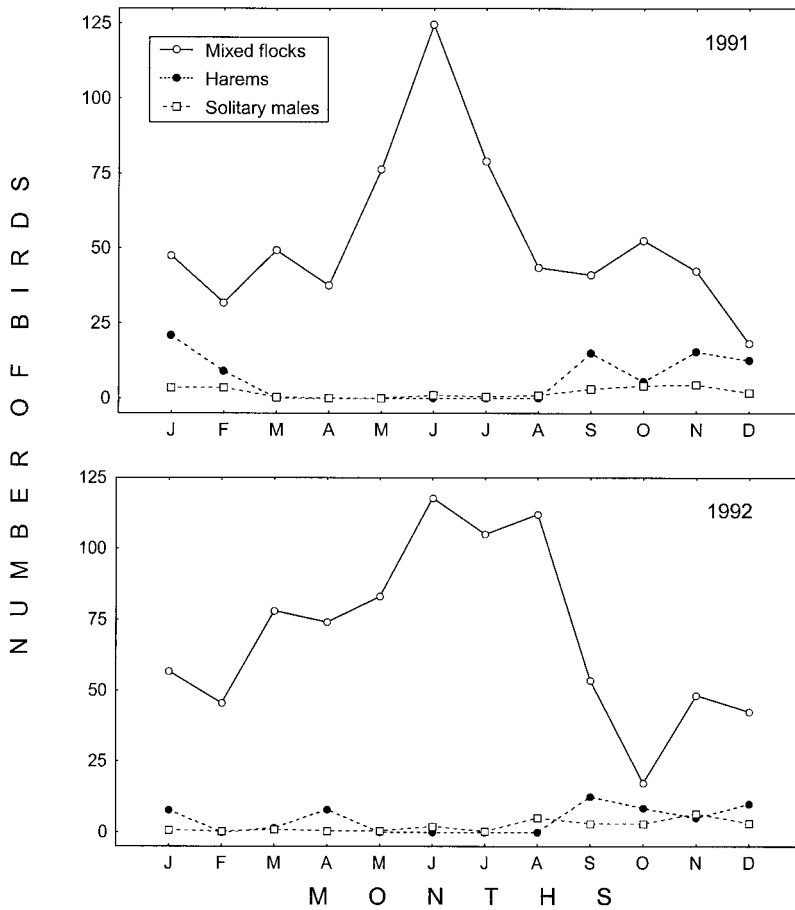


FIG. 1. Mean monthly number of individual Greater Rheas which, during 1991 and 1992, integrated into mixed flocks or harems or were solitary males.

ior, feeding, and locomotion were not significant.

Pairwise comparisons of the rates of social behavior by adult males showed an increase in the levels of courtship and alert postures from the phase of solitary male to subsequent phases (i.e., harem formation and harem; courtship: $n = 16$, $Z = -3.5$, $P < 0.005$; $n = 16$, $Z = -3.5$, $P < 0.001$; alert: $n = 16$, $Z = -3.4$, $P < 0.005$; $n = 16$, $Z = -3.3$, $P < 0.005$, respectively; Wilcoxon signed-ranks test), a decrease in calling from the first two phases (i.e., solitary male and harem formation) to that of harems ($n = 16$, $Z = -2.9$, $P < 0.01$; $n = 16$, $Z = -3.4$, $P < 0.005$, respectively), and a gradual decrease in harem defense (solitary male vs. harem formation and harem: $n = 16$, $Z = -2.7$, $P < 0.01$; n

$= 16$, $Z = -3.5$, $P < 0.005$, respectively; harem formation vs. harem: $n = 16$, $Z = -3.2$, $P < 0.005$) and male expulsion (solitary male vs. harem formation and harem: $n = 16$, $Z = -3.5$, $P < 0.005$; $n = 16$, $Z = -3.5$, $P < 0.005$, respectively; harem formation vs. harem: $n = 16$, $Z = -3.5$, $P < 0.005$) among the three phases. The rate of male-male fighting increased from the phase of solitary male to that of harem formation ($n = 16$, $Z = -2.9$, $P < 0.01$), and then decreased during the phase of harem (solitary male vs. harem: $n = 16$, $Z = -2.5$, $P < 0.05$; harem formation vs. harem: $n = 16$, $Z = -3.3$, $P < 0.005$; Fig. 2).

Once the harems were established, the males' behaviors varied from the beginning to the end of this phase. Courtship, harem defense, male expelling, calling, and male-male

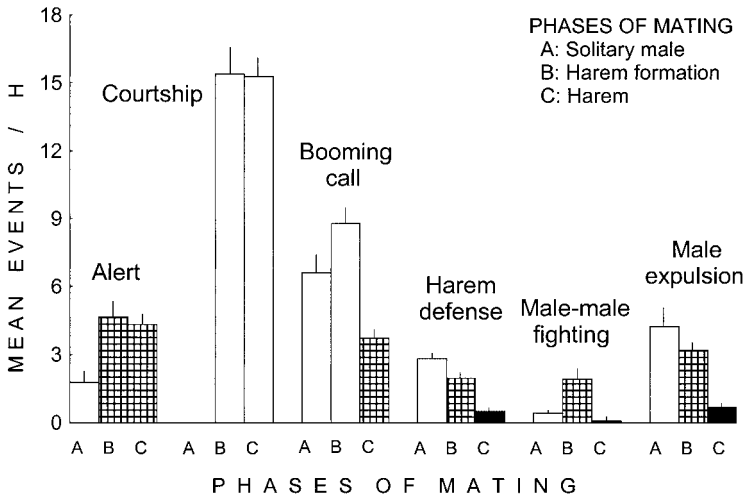


FIG. 2. Mean (+SE) rates of all social activities recorded for 16 adult male Greater Rheas observed in Rio Grande do Sul, Brazil, 1990–1992, during the phases of solitary male (A), harem formation (B), and harem (C). Bars with the same shading within each particular activity represent statistically similar rates (i.e., nonsignificant differences: $P > 0.05$; Wilcoxon signed-ranks tests).

fighting decreased from the first to the second half of this period, with the last two activities vanishing altogether (Table 1). There were no significant changes in the rates of nonsocial behaviors.

Five copulations were observed and these took place between adult males and females of their own harems, and occurred during the harem phase.

DISCUSSION

Because of the lack of a relationship between the rate of rhea nonsocial activities and the phases of mating, we concentrate our discussion on social interactions (alert posture may be considered as both social and nonsocial,

since it may be directed toward conspecifics and/or toward the environment). Our observations of the occurrence of aggressive interactions early in the mating period and of courtship once the harem has been acquired agree with Bruning's (1974) report of Greater Rheas living in Argentina. In our study, although all three types of aggression decreased to their lowest levels in the harem phase (and especially in its second half), harem defense and male expulsion were highest at the beginning of the mating process (after which they gradually decreased), whereas male-male fighting reached its highest rate during harem formation. This matched our prediction that the highest rates of aggressive behavior

TABLE 1. Mean (\pm SD) rates (events/h) of the activities of 16 adult male Greater Rheas during the first and second halves of the harem phase, Rio Grande do Sul, Brazil, 1990–1992.

Behavior	1st half	2nd half
Comfort behaviors ^{ns}	2.61 \pm 1.00	3.88 \pm 3.33
Feeding ^{ns}	55.10 \pm 19.52	74.06 \pm 34.75
Locomotion ^{ns}	95.21 \pm 49.06	122.92 \pm 95.45
Alert posture ^{ns}	4.76 \pm 1.55	5.21 \pm 0.36
Courtship ^{**}	21.90 \pm 4.78	8.63 \pm 8.54
Calling ^{**}	7.02 \pm 2.30	0
Harem defense ^{**}	0.77 \pm 0.39	0.03 \pm 0.77
Male-male fighting [*]	0.25 \pm 0.22	0
Male expulsion ^{**}	1.04 \pm 0.40	0.16 \pm 0.21

^{ns} Not significant, ^{*} $P < 0.05$, ^{**} $P < 0.03$; Wilcoxon signed-ranks tests.

should occur when the resource (the harem) was being acquired, i.e., while obtaining maximal benefits but reducing the risks of injury at other times. Thus, male Greater Rheas limit their engagement in the riskiest behavior, aggressive elimination of competitors, to the phase of harem formation, when they also initiate courtship.

Booming calls apparently function mainly in relation to aggressive competition between males, as it often occurs in association with male-male chasing and fighting, but seldom during courtship. The same conclusion was reached by Bolwig (1973) for the booming call of the male Ostrich (*Struthio camelus*), the rhea's closest relative within the ratites (Cracraft 1974, Sibley and Ahlquist 1990). The pattern of booming call variation through the mating phases was similar to Bruning's (1974) report of a decreased level of booming once harems became established.

Courtship behavior, as defined above, was absent early in the mating period, showing an opposite pattern of variation compared to male-male aggression through the phases of mating. In that respect our results do agree with those of Bruning (1974), although the short duration of his observations during the harem phase (7–9 d) and the low number of subjects (two captive and two wild males) limit the significance of his data.

In regard to the low number of copulations observed in this study, Bruning (1974) observed that viable sperm was stored in the female's oviduct for at least 8 d, and probably longer, suggesting that in rheas a low number of sperm might be sufficient to assure fertilization of the whole clutch of each female. Although we might expect a high rate of copulation in polyandric populations due to higher intermale competition (Birkhead et al. 1987), this should not apply to sequential polyandry (the case of the Greater Rhea), in which male mates do not coincide in time, except if there is sperm storage.

The higher level of alert behavior during the last two phases of mating suggests that this behavior may be directed toward potential competitors and/or toward mates, although its similar rate, during both halves of the harem phase, and the observation of frequent scan-

ning of the area by males in all seasons, also suggest a likely function of antipredator defense.

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