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Rhea americana

Greater Rhea   ORDER: STRUTHIONIFORMES | FAMILY: RHEIDAE | POLYTYPIC 5 SUBSPECIES

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Life History

Food

Grasses and insects provide the staples of the Greater Rhea's diet. Their huge caecum and colon may act as fermentation chambers producing volatile fatty acids, digesting hemicellulose and cellulose with the help of bacteria (Martella et al. 1996; Sales 2006).

In agricultural areas Greater Rheas eat mostly alfalfa and wild dicots, with no preference for grasses. Rheas consume higher proportions of alfalfa in the winter, when the resource is too short to be used by cattle, and thus pose no competition for cattle grazing opportunities (Martella et al. 1996).

Early reports of rhea diets also mention the consumption of berries (Stenjneger 1885), and snakes and rodents (Peterson 1963: 179). Rheas twice have been reported pecking at fresh fecal matter dropped by other rheas. One such bird proceeded to walk away and wipe its bill on grass, a movement common in passerines but not previously reported in rheas (Raikow 1968).

Raikow (1968) also reports two occasions in which rheas tried to catch small birds, including a vividly described scene in which a captive rhea succeeded in killing and eating a Common Grackle *(Quiscalus quiscula)* in the Detroit Zoological Park. After an excited period of running around its enclosure during which it stopped often to rub its prey in the dust even after the grackle had stopped moving, the successful predator ran off with its prey after attacking another rhea who attempted to steal it. After 15 excited minutes of extreme vigilance, it ate pieces of meat torn off the grackle by pecking and shaking it in the air. With vigorous head-shaking the rhea was able to swallow the remnants whole (Raikow 1968).

Dietary breakdown of wild Greater rheas

(from Martella et al. 1996):

Green material: 90.1%

Seeds: 8.9%

Fruits: 0.6%

Insect fragments: 0.1%

Vertebrates: <0.1%

Chick nutrition

Feeding captive chicks either 0.7 or 1.4% dietary calcium has been shown to improve growth rates without causing bow leg syndrome (Bastos et al. 1999).

On this page...

Food

Behavior

Territoriality

Sexual Behavior

Social and interspecific behavior

Predation

Reproduction

Populations and Demography

Morata et al. (2006) analyzed the metabolizable energy values and digestibility of dry and organic matter in several feed ingredients produced in Brazil, using the total collection of feed intake and excreta output or external marker chromium oxide on 7 month old Greater Rheas. This information may prove useful in determining the optimal cost-effective feed formulation for captive birds.

Behavior

Posture

Standing- One foot stands about twelve inches behind the other. One leg angles slightly, supporting less weight than the other, held vertically.

Crouching- The weight rests on the heels and partially on the toes. Tibia converge downward making contact.

Sitting- Knee and heel joints flex completely, making the tibia and tarsi parallel. The neck may extend straight out on the ground or fold into an S-curve.

Crouching- Usually a rhea crouches very briefly on the way to sitting, but may maintain the crouch posture for several minutes to preen or dust-bathe.

Feeding

Ambulatory food-searching occupies much of the Greater Rhea's time. It forages while walking slowly, holding the head lower than 50 cm above the ground, interrupted by occasional bouts of vigilance in which they will raise their heads and scan the area. With its neck curved into a U, the rhea moves slowly, scanning up and down or side to side with small motions of the head. Once it finds a food item, a rhea will pick it up with the tip of its bill, jerk its head back a few inches, throw the food up into the air and catch it in the back of its mouth with a forward thrust of its open bill. This motion is performed regardless of food size. For a few seconds after, the rhea will raise its neck vertically, and scan from side to side, probably to facilitate swallowing while taking the opportunity to search for danger (Raikow 1968, Gussekloo and Zweers 1997, Gussekloo and Bout 2005). The body remains relatively stationary while feeding (Van der Leeuw et al. 2001).

Beaver (1978) studied the ontogeny of feeding and drinking, and outlined the following sequence of motions performed by feeding chicks: orientation, pecking thrust, head lift, forward head jerk, swallow. He found that efficiency of responses develops with experience.

Drinking

Rheas drink by extending their necks to scoop water with their bills, pulling out about six inches, then thrusting their heads forward to capture the water pulled into the air by the backward movement. If the water surface is too small, they will drink using pecking motions (Raikow 1968, Beaver 1978b, Gussekloo and Bout 2005). This is most often performed while standing. A rhea may take a quick drink at any time, and will drink for longer periods of five to ten minutes before or after a long period of feeding, or soon after awakening. Water in the digestive tract may inhibit feeding for a few minutes (Raikow 1968).

Preening

Brief preening breaks may intersperse feeding and resting bouts, but long periods of preening typically precede or follow settling down for a nap. One or both wings spread laterally, with the humerus extended laterally and the radio-ulna pointing downward, directing the dorsal wing surface anteriorly with an upward point of the elbow, a posture also adopted in the male Wing Display. While preening the neck bends back over the humerus, and the bill moves among the feathers from the underside, which has a bare surface in comparison to the dorsal surface covered with small feathers impeding a full range of preening.

The rhea focuses most of its preening efforts on its wings., where there are many feathers,

and long primary and secondary shafts that easily misalign due to wind, body contact, and movement during running, displays, and preening of other body parts. Preening the wings serves as displacement activity following courtship and aggressive encounters. The neck and tibiae require significant preening, but the sparsely feathered back, rump, and flanks require little. Rare nibbles at the unfeathered tarsus may remove loose pieces of scaly skin. A rhea must preen the generally loose plumage of its wings three times as often as its neck, while a typical passerine devotes equal time to both.

Vigilance

As group size increases, birds spend less time being vigilant and more time feeding. Individuals foraging alone must devote more time to vigilance and less to feeding than those foraging in groups. During the breeding season, both sexes spend less time feeding and more time in bouts of vigilance, and males have shorter feeding bouts than females (Reboreda and Fernandez 1997).

Both sexes are more vigilant in higher vegetation (Martella et al. 1995).

The more rheas in a group, the less time each rhea spends in vigilance. While individual scanning rate decreases with increasing group size, the length of each scan event remains constant, and the timing of such events deviates slightly but significantly from random (Carro and Fernandiz 2008).

Locomotion

Rheas are suited for life in wide plains, using long, strong legs to cover distance quickly. The rhea generally ambles at a leisurely pace, running only during social activities (Raikow 1968). The head moves back and forth slightly along the sagittal plane as the rhea walks, a common movement among birds that may give mechanical assistance to walking and aid in visual fixation on surroundings (Daanje 1950).

The rhea uses the stretched limb model of walking, whereas the kiwi uses the crouched limb model (Abourachid 2001). While walking or running, rheas tend to cross their feet, even during a straight trajectory (Abourchid and Renous 2000).

During sexual or agonistic encounters, a rhea runs crouching, moving the wings and neck, and ruffling the plumage. Captive rheas running to be fed by spectators hold the neck vertically, wings only slightly raised, with no ruffling of plumage (Raikow 1968). Running increases body temperature and the rhea must manage its body temperature by storing heat (Taylor 1971).

Dust Bathing

A dust bath may precede a period of rest. While crouching or sitting the rhea picks up dust or dirt with its bill, retracts its neck into an S-curve, and tosses its head towards either of its wings, folded over its back. During less intense bouts, it drops the dust beside itself instead of onto itself. It spends several minutes dust-bathing and preening, then settles to sleep. For the first few minutes of sleep it may awaken to listlessly scoop and drop dust in place before returning to sleep. Many birds, including Ostriches and many passerines, thrash dust vigorously through the feathers, ostensibly to remove external parasites. It is unknown whether the more tranquil motions of the rhea have any similar effect; it may serve a displacement function, being performed mostly by males (Raikow 1968).

Sleep

Greater Rheas sleep with the neck in an S-shaped loop, resting the bill on the throat (Raikow 1968). Juveniles sleep almost exclusively at night and rarely during the day (Amlaner et al. 2001, Steele and Amlaner 2004).

Miscellaneous

A rhea will defecate most often while feeding and occasionally while drinking.

Scratching the head requires extending the neck forward and down until it hovers a few inches over the ground, at which point a foot extends to scratch vertically eight to ten times.

While standing or walking, a rhea often shakes or stretches its wings. Sometimes a wing stretches laterally to one side while the opposite leg extends backward. Innumerable slight twitches may jolt through the head, wings, body, and skin at any time (Raikow 1968).

Territoriality

During the breeding season, nesting males defend their nest sites from other males. Soon after females begin laying in his nest, a male becomes increasingly aggressive towards any rhea approaching, including females, and eventually he drives them away.

Sexual Behavior

Overview

The Greater Rhea exhibits a suite of reproductive behaviors that are unusual among birds. Harems of females lay communally for a series of males, and occasionally surround a male to perform cooperative group copulation solicitation displays. Males incubate and care for the chicks alone, although occasionally a younger subordinate helper will incubate the first clutch ostensibly fathered by the older dominant male, freeing him to establish and incubate a second clutch. Joint nesting sometimes occurs, in which two males nest less than a meter apart and peacefully steal each others' eggs, sharing the duties of parental care upon hatching. Males leading broods of chicks sometimes adopt younger orphan chicks separated from their original brood.

A very small proportion of males attempts to breed each year, and the few that try frequently abandon their nests, particularly early in the breeding season. Although the most dominant and experienced males presumably breed earlier, nests started later in the season succeed at greater rates. Genetic analysis of parentage is necessary to determine whether realized reproductive success actually follows this atypical pattern. Females can retain viable sperm in the oviduct for eight days or longer (Bruning 1974), and though earlier breeding males suffer lower rates of nesting success, it is likely that they father eggs laid in the nests of later breeding males, offsetting the costs of early nest failure and abandonment. Later breeding males have less chance of establishing a second clutch if they abandon their first, and less chance of fathering a proportion of subsequent clutches, and should abandon less often despite higher degrees of paternal uncertainty.

Mating System

The Greater Rhea has one of the strangest mating systems of all birds, and is one of the few species with exclusive paternal care. Bruning (1974) conducted the first field study in Buenos Aires, Argentina, publishing a thorough description of the observable social system that provided the foundation for two later studies on rhea reproduction by Codenotti and Alvarez in Rio Grande do Sul, Brazil, between 1990 and 1992, and Fernández and Reboreda in Buenos Aires, between 1992 and 1995.

Females copulate and lay eggs in a nest built by a single male, then wander away with no further role in reproduction. A male must defend his nest site and harem, build a nest, perform courtship displays, incubate the eggs, and care for the chicks alone. This system has been described as simultaneous polygyny with sequential polyandry, in which a harem of females lays consistently in the nest of one male then moves to lay consistently in the nest of another, associating exclusively with a sequence of up to twelve different males. The order in which the males associate with a harem presumably reflects a dominance hierarchy determined by age and/or the outcomes of aggressive interactions (Bruning 1974, Handford and Mares 1985, Fernández and Reboreda 1998, Martella et al. 1994, Lábaque et al. 1999).

However, a study of marked birds by Martella et al. (1998) suggests an even more

complicated picture. Males in this study fell into four progressive categories, apparently according to age rather than aggressiveness: (1) non-reproductive males, (2) males that only incubate, (3) males that copulate and incubate, and (4) males that copulate only. Females are inseminated by a succession of males and eventually lay in whatever nests are available to them, not necessarily those of the males they have most recently copulated with (Davies 2001). This promiscuous system of communal laying across several nests and extensive extra-pair copulation results in a high degree of parental uncertainty and effective cooperative care.

A very small proportion (20%) of males attempts breeding each year, and only 5% of males successfully breed chicks surviving to 2 months old (Fernández and Reboreda 1998). This small number of incubating males imposes a bottleneck on available parental care, further obscuring paternity from rheas and researchers alike.

During the non-breeding season rheas forage in mixed flocks of 4-35 male and female birds of all ages. From August through November, adult males fall behind the flock and follow at a distance of 30 to 300 m for about 25 days. They return to the flock for the next month, fighting other males, courting, and associating with a harem of 2-12 females. During spring, a harem and a single male leave the flock to stay in a defended nesting site for 30-45 days (Codenotti and Alvarez 2001).Females within the same harem lay communally in the same nest built by the male. A female can lay every other day for 10-15 days, yet clutch size does not vary with harem size, suggesting that only a small core of females in a harem actually lay eggs in a clutch (Bruning 1974, Fernández and Reboreda 1997, 1998). Females in a single harem sometimes perform a complex cooperative copulation solicitation display in a closed circle around the male (Fernández and Mermoz 2003). Genetic analysis of parentage will determine what proportion of females actually lays and the realized reproductive output of each female across clutches in a season. If females within a harem are related, kinship may explain why females breed communally and occasionally cooperate in group copulation solicitation displays.

Sperm remain viable in the oviduct for at least 8 days and probably longer (Bruning 1974). With such a long period of sperm retention, and the tendency of females to lay in the nests of several different males, it is likely that nests with eggs laid later in the season may contain eggs fathered by males other than the incubator. Thus certainty of paternity and total reproductive output across clutches are expected to decline with position in the breeding order.

Incubation and Cases of Joint Nesting

Males begin incubating two to three days after the females begin laying, becoming increasingly aggressive towards any approaching rheas, and eventually driving the females away. Males almost always breed alone and aggressively expel other males from their nesting sites. However, two studies have reported intriguing cases of peaceful male partnerships including apparent cases of cooperative breeding. Fernández and Reboreda (1995) describe four cases in which two wild males nested less than 1 m apart and periodically stole eggs from each other throughout the incubation period. In each case a second male sat beside the nest of a male already incubating and began stealing eggs, instigating a peaceful clandestine exchange. All cases occurred at the end of the breeding season, when access to sexually active females had decreased. After hatching, both males shared the care of the chicks (Fernández and Reboreda 1995).

Cooperative Breeding

Cooperative breeding between pairs of males has been reported in Brazil by Codenotti and Alvarez (1997). Of 35 observed harems, 8 contained a dominant male as well as a younger subordinate from the same original flock. Dominant adults in these two-male groups defended the harem, made territorial calls and aggressive displays, and expelled other

males from the area more often than males without helpers. However, they invariably tolerated the presence of their subordinate helpers. Females approached the dominant males 656 times and the subordinate males 48 times, and while the dominant males appeared significantly more reproductively active, it is possible that the subordinates garnered occasional reproductive opportunities.

In such cases, a dominant male builds a nest in which the females lay, leaves the subordinate to incubate it, and establishes another nest in which the same females lay a second clutch that he incubates himself. In the recorded cases, both broods had relatively equal hatching success, and the combined clutch sizes laid by harems with two males were roughly equivalent to those laid by harems with single males. More chicks survived to 5 months in broods led by the dominant males (75%) than in broods led by subordinate males (17%), but overall survival rates were higher than in broods of solitary males (22%) (Codenotti and Alvarez 1997).

The duties of incubation and chick rearing incur costs, reducing feeding periods and increasing risk of predation (Fernández and Reboreda 1998). The dominant males in such partnerships may benefit from increased chick survivorship, but the benefits to the subordinate helpers remain unclear. This is one of the principle questions in cooperative breeding literature, and four hypotheses are typically considered: (1) direct reproductive success by fathering some young, (2) indirect reproductive success through kin selection, (3) gaining reproductive experience increasing future success, (4) higher reproductive status if females recognize and value helping behavior. The second hypothesis proposes helpers may gain inclusive fitness benefits by caring for the young of close relatives, and has been studied in several other species of cooperatively breeding birds. Survivorship data coupled with genetic analysis can address the first two hypotheses by determining whether the subordinate fathers a proportion of the combined clutch, what proportion survives, and whether the two males are related and therefore are subject to inclusive fitness benefits.

Social and interspecific behavior

Greater Rheas may forage individually or in groups of up to 50 birds during the non-breeding season (Reboreda and Fenandez 1997). The start of the breeding season marks a sharp change in social behavior. Single males break away from the flock and follow at a distance, females form harems of between 2-12 birds, and yearlings mix with males that do not attempt breeding to form large non-reproductive flocks (Bruning 1974, Hanford and Mares 1985).

Predation

Rheas are subject to high predation throughout their lives.

Mercolli and Yanosky (2001) conducted intensive ecological studies at El Bagual Ecological Reserve in northeastern Argentina, where they witnessed five cases of predation by cougars (*Felis concolor*) and one by a dog.

Between June and August 1991 cougars captured one adult male and four adult females in open *Paspalum* grasslands, as evidenced by the discovery of blood and feathers dragged to the nearest woodlands, and partly buried, with open abdomens and little viscera consumed.

In October a 12 kg domestic dog attacked a juvenile rhea in grassland, opened its abdomen, and partially consumed the viscera. The juvenile sustained injuries to the legs and head, most likely while attempting to escape through the perimeter fence while chased.

In December and January, two broods of 2-3 month-old rhea chicks were found dead but uneaten, with many bite-like wounds on their skins. Cougar kittens had been sighted twice during the same period, and the wounds on the dead chicks suggested they had been killed by cougar kittens learning to hunt.

In November, two nests were found partially buried in an ecotone between a *Paspalum*

grassland and humid mature forest, with 8 and 9 eggs respectively destroyed by a six-banded armadillo (*Euphractus sexcinctus*) that had burrows below the nests where eggshells were found. When the nests were first found they were not over armadillo burrows, suggesting that the armadillos dug burrows under the nests after laying. Both fathers abandoned the nests.

Observed predation on adult wild rheas occurred during harem formation and courthsip (July-August). Reduced vigilance during the breeding season may put rheas at greater risk of predation during this time.

Conservation and reintroduction plans should consider the cougar a limiting factor of wild rhea populations, and address the currently unstudied effect of the increasing six-banded armadillo population on nesting success (Mercolli and Yanosky 2001).

Puma and jaguar predation was reported in the Paraguayan Chaco (Taber et al. 1997), and in central areas of Bolivia and Brazil (Eisenberg and Redford 1999, Oliveira 1994). Carnivore researchers report puma predation on rheas at Serra da Canastra and Emas National Parks in the Brazilian Cerrado. Mustelids have been reported as predators in Brazil (Codenotti 1997).

Reproduction

The nest is on the ground. The male selects a site, and tramples the surrounding vegetation with his feet. The male then sits on the site of the nest, rotating slowly in a circle while pushing backwards with the feet, raising a mound about 1.4 m across (range 1-2 m, *n*=87) with an interior depth of ca 30 cm. The nest scrape is lined with grass, which the male gathers with his bill (Bruning 1974).

Eggs are elliptical and shiny in texture. Fresh eggs are golden in color, but become white after being exposed for 5-6 days to the sun (Sick 1993). The mean clutch size of nests at one site in Argentina was 26.1 (Bruning 1974). Average mass of the egg is 605 g (Mato Grosso; Sick 1993).

The mean length of incubation at one site in Argentina was 36.6 days (Bruning 1974).

Breeding success in the Greater Rhea is remarkably low. Following the fate of 34 nests, Bruning (1974) found that only 7 (20%) hatched any chicks. From 119 eggs in the five nests of known clutch size, 74 chicks hatched (62%). Another study in Argentina followed 162 nests over the course of four years. Only 52 (31.7%) hatched any young (Fernández and Reboreda 1998). Nests established late (November and December) succeed more often than earlier nests (September and October). In most bird species, early nests succeed more often than late nests, and the cause of the rhea's pattern of increasing success rates is likely related to the high rates of nest desertion. Males desert 65% of their clutches. This may be due to egg predation, egg breakage, disturbances by people, livestock, or predators, or hot or rainy weather, but males will sometimes desert for no apparent reason (Fernández and Reboreda 2002).

Fernández and Reboreda propose that the seasonal increase in nesting success may be due to differences in quality between early and late breeders, and/or seasonal environmental variation. Higher nesting success of later breeders does not necessarily imply higher reproductive success due to diminished certainty of paternity, possible lower rates of chick survival, and the possibility that early deserters may renest, and conclude that there is at present no clear explanation for seasonal increase in nesting success and its correlation with reproductive success.

Populations and Demography

Population genetic variation

Phenotypic analysis of randomly amplified polymorphic DNA markers sampled from four isolated wild populations in Argentina revealed that over 94% of total observed molecular variance was due to differences within populations, and only 6% due to differences

between separate populations. Recent population fragmentation and isolation may have contributed to genetic drift and inbreeding, increasing local genetic variation and decreasing variation within populations (Bouzat 2001).

Distribution

Conservation

Recommended Citation

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