ADOPTION OF UNRELATED YOUNG BY GREATER RHEAS

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Abstract.—The benefits, if any, of the adoptive behavior of male Greater Rheas (*Rhea americana*) towards unrelated young while leading their offspring are not known. Therefore, we quantified adoption by Rheas in an agricultural area of Rio Grande do Sul, Brazil, in order to quantify the potential benefits and the recipients of these benefits. Adult males frequently adopted (23%), were more vigilant and protective than non-adopters, and ended up leading larger groups of young than non-adopting males. The adopted chicks were usually not more than 1-wk old and survived in greater proportion than the adopter's own offspring.

ADOPCIÓN DE POLLOS EXTRAÑOS POR EL ÑANDÚ *RHEA AMERICANA*

Sinopsis.—De existir ventajas en la adopción de pollos extraños por parte de machos adultos de Ñandú (*Rhea americana*), se desconocen los posibles beneficiarios. Las observaciones realizadas en un área agrícola de Rio Grande do Sul (Brasil) se orientaron a determinar los posibles beneficios y la identidad de los receptores. Los machos adultos adoptaron frecuentemente a pollos extraños (23%), fueron más vigilantes y más protectores que los machos no adoptadores y acabaron dirigiendo mayores grupos de pollos. Generalmente los pollos adoptados tenían no más de una semana de edad y sobrevivieron en mayor proporción que los pollos propios.

Adoption of unrelated offspring in birds has attracted much attention because this apparently altruistic behavior benefits unrelated individuals. The benefits of adoption to strayed or orphaned chicks are evident, and it also may be adaptive for young receiving inadequate parental care to seek adoption by switching to broods where they receive better care (Bustnes and Erikstad 1991, Hébert 1988, Holley 1981, Pierotti and Murphy 1987, Redondo et al. 1995, Savard 1987). Foster parents could obtain some benefits by gaining reproductive experience (Riedman 1982) or increased competitive ability through increased family size (Williams 1994), or adopting males could gain access to copulations with mothers of the adopted young (Martin 1989). Adopters might obtain benefits for their offspring by exploiting the adopted young (e.g., through increased awareness of predators or by diluting the risk of predation through a "selffish herd" effect; Hamilton 1971, Pierotti 1988, Riedman 1982). Indirect benefits through kin selection could be obtained by the foster parents if the adopted young are close relatives (Riedman 1982, Waltz 1981). Reciprocal altruism would be involved if fostering is reciprocated by the adoptee's genetic parents (Pierotti 1980, 1982, Riedman 1982). Finally, in some cases, adoption has been attributed to reproductive errors or maladaptation (Birkhead and Nettleship 1984, Bustamante and Hiraldo

1990, Carter and Spear 1986, Donázar et al. 1991, Plissner and Gowaty 1988).

According to the intergenerational conflict hypothesis (young trying to obtain adequate parental care from unrelated adults and the latter trying to avoid providing such care whenever there is a potential cost to it), chicks seeking adoption would be expected to win against adults discriminating against them because (1) selection on the offspring will often be stronger (surviving versus dying) than on the adults (saving versus losing some reproductive effort and, perhaps, some residual reproductive value) and (2) selection will act most strongly on an early than on a later life stage because the fitness consequences of early selection are much greater (Pierotti 1991).

For species with precocial young, adoption may entail few costs (if young are not fed, there is no additional costs to guarding adopting offspring) and some (above-mentioned) potential benefits for alloparents. Under this circumstance adoption is common (Pierotti 1988, Savard 1987) since chicks not guided or protected adequately by their genetic parents would be expected to switch to a better brood, and alloparents would not be expected to discriminate against them. On the other hand, if alloparents would benefit from adoption, we should expect the most qualified individuals to incur the burden of adoption.

The Greater Rhea (*Rhea americana*) has precocial young. After joint nesting by a group of females, the male incubates the large clutch of eggs while the females move on to another male's territory in a sequential polygynandry fashion. As the male leads his brood, guiding and protecting it, he often collects stray chicks, until he is followed by a group of young whose ages vary (Bruning 1974, Codenotti 1995). The facts that male Greater Rheas often adopt a large number of offspring (as compared to only 1–2 in most other species) and that adoptees' age is often quite different from that of genetic young and are kept for a long period of time renders the species specially suitable to investigate several aspects of adoptive behavior. The observations reported in this paper try to quantify the potential benefits (and the recipients) of adoptive behavior in the Greater Rhea, and whether better quality males are more likely to adopt and are more attractive to offspring seeking adoption.

STUDY AREA AND METHODS

This study is based on observations of free-ranging Greater Rhea living in a farming area (1980 ha) with natural and cultivated meadows, crops (wheat, soybean, oats and maize), and livestock (cattle and horses) in Rio Grande do Sul, Brazil (28°4'N, 52°22'W). Observations were made during the breeding seasons (August–February) of 1990–1992, when the population varied from about 90 to 140 adults and the density of broods was 0.01–0.06/ha.

The study area was explored at least once a week. All males (individually recognizable based on differences in body size and plumage, Codenotti 1995) were monitored individually during their reproductive cycles.

Whenever a male was found accompanied by young, it was identified and the number and estimated age (Codenotti 1995) of his offspring and of adopted young (recognized according to records throughout the brood period of the number of young of each age accompanying each male) was recorded. In all, 39 groups of males with young were recorded along the three years of study.

Focal 15-min observations were made of the behavior of the 22 males in charge of broods, 7 and 15 of them being adopters and non-adopters, respectively (186 h equally distributed among individuals), and of randomly chosen chicks in the seven broods including adopted young (10 offspring and 12 adopted chicks received 47 h of observation). The activities recorded for the males were comfort behavior, feeding, locomotion, sheltering young, gathering young, leading brood, attacking other Rheas, and fleeing from danger. Behaviors for the young were maintenance, feeding, running, walking steady before or behind the male, playing, and pecking at other chicks (for descriptions see Codenotti et al. 1995).

Of the 22 broods, the 7 adopting broods were monitored until the male's offspring were 90–180-d old, and all of them for at least 60 d after the date of adoption. Of the 15 non-adopting broods, 11 were monitored until the chicks were 90-d old.

RESULTS

Out of 39 groups of males with 285 young recorded in the three years, 9 of them (23%), each led by an adult male, included some adopted young.

We were able to observe the act of adoption on four occasions. In three of them lost chicks produced a high-pitched distress call (Codenotti et al. 1995) that attracted the attention of the male with a brood passing nearby. The males responded with their gathering sound (a clatter of the upper and lower mandibles). The males and the stray chicks looked for each other and the chicks merged into the broods, keeping themselves near the male and not suffering any aggression from the brood members. The adopted chicks originally became lost from their father's brood because of human or predator (Crested Caracara *Caracara plancus* and Pampas Fox *Dusicyon gymnocercus*) interference (the chicks run in all directions and those not following the fleeing male were lost if the male did not return later on to gather them), or they might remain feeding in one place while the brood resumed walking. The other case of adoption observed did not involve stray chicks. After two broods (one of them lead by an adult male and the other by a helper subadult of another breeding unit; Codenotti and Alvarez 1997) foraged near each other for 13 d, 5 of the 12 subadult's young joined the adult's brood of 15 when the two groups separated.

Table 1 shows the number and age of offspring in the seven adopting broods. The adopting male's offspring were ≥30-d old ($\bar{x} \pm SE = 47.96 \pm 6.39$ d, $n = 7$) and the adopted chicks were, with the exception of one

TABLE 1. Number, estimated age, and survival to 60 d post-adoption of offspring and of adopted chicks in seven adopting broods at Rio Grande do Sul, Brazil (1990–1992).

Males	Date of adoption	Offspring			Adopted chicks		
		Number at adoption	Age at adoption (d)	Number surviving	Number adopted	Age at adoption (d)	Number surviving
A	28 Feb. 1991	11	30	3	4	7	2
B	16 Dec. 1992	8	60	8	1	60	1
C	28 Mar. 1991	4	60	2	4	7	2
D	2 Feb., 8 Feb., 13 Apr. 1991	15,15,12	60,60,80	10	5,15,18	20,7,7	38
E	14 Feb.1992	15	30	11	5	7	4
F	18 Feb.1993	18	60	3	5	7	3
G	26 Feb. 1993	23	30	7	4	7	4

TABLE 2.   Rates per minute ($\bar{x} \pm$ SE) of the behavioral activities recorded for the 7 adopting (when already accompanied by their adopted young) and the 15 nonadopting males.

Activities	Adopting males	Nonadopting males	Mann-Whitney Test	
			U	P
Comfort behavior	0.08 ± 0.02	0.07 ± 0.02	48.5	0.776
Feeding	0.62 ± 0.19	0.77 ± 0.17	46.5	0.672
Locomotion	0.91 ± 0.20	0.93 ± 0.13	51	0.439
Vigilance	2.46 ± 0.38	1.29 ± 0.19	19	0.018
Sheltering chicks	0.06 ± 0.02	0.03 ± 0.01	24.5	0.045
Gathering chicks	0.11 ± 0.03	0.08 ± 0.02	34	0.189
Leading brood	0.29 ± 0.09	0.08 ± 0.02	17	0.012
Attacking strangers	0.02 ± 0.01	0.01 ± 0.00	23	0.026
Fleeing	0.06 ± 0.02	0.07 ± 0.01	41.5	0.435

brood, younger (14.81 ± 7.53 d, $n = 7$) than the male's own offspring and usually not more than 1-wk old.

Mean brood size of adopting broods before adoption was not significantly different from that of non-adopting broods (13.0 and 10.6, respectively; $n_1 = 7$, $n_2 = 15$, $P = 0.395$, Mann-Whitney test). Adopted young composed 37% of the post-adoption brood. Mean brood size after adoption was 23.3.

The seven recorded adopting males were more vigilant, sheltered young more often, and attacked strangers more frequently than the 15 recorded non-adopting males (Table 2). In the seven adopting broods genetic offspring fed and walked before and behind the male more often, and walked side by side with the male, played and pecked at other chicks less often than adopted chicks (Table 3).

In the seven adopting broods, adopted chicks survived to 60 d after adoption in greater proportion than natural offspring in adopting broods ($P < 0.04$, $n = 7$, Wilcoxon test). The proportions of natural offspring surviving from hatching to the age of 90 d were not significantly different

TABLE 3.   Rates per minute ($\bar{x} \pm$ SE) of the behavioral activities recorded for randomly-chosen offspring and adopted unrelated chicks in the seven adopting broods.

Activities	Offspring ($n = 10$)	Adopted ($n = 12$)	Wilcoxon Test	
			Z	P
Comfort behavior	0.34 ± 0.05	0.43 ± 0.04	−1.44	0.150
Feeding	6.69 ± 1.40	3.22 ± 0.33	−2.03	0.042
Running	1.07 ± 0.08	0.85 ± 0.18	−1.01	0.310
Walking steady	0.33 ± 0.04	0.79 ± 0.09	−2.37	0.018
Walking before	0.80 ± 0.07	0.35 ± 0.04	−2.37	0.018
Walking behind	0.83 ± 0.07	0.22 ± 0.03	−2.37	0.018
Playing	0.21 ± 0.04	0.58 ± 0.07	−2.37	0.018
Pecking	0.35 ± 0.14	0.12 ± 0.02	−2.21	0.027

for the 7 adopting and the 11 monitored non-adopting broods ($P = 0.65$, Mann-Whitney test).

<div align="center">DISCUSSION</div>

Greater Rhea chicks are adopted mostly at the age (0–10 d) when they stray most often from their fathers' broods and when they suffer the most from predation (Codenotti 1995). Because lone chicks are unlikely to survive, it is clearly adaptive for them to look for care and protection in another male's brood. This recalls the situation for semi-precocial gulls and terns, whose chicks seek adoption in foster broods when they have low chances of survival (Graves and Whiten 1980, Morris et al. 1991, Pierotti and Murphy 1987).

Furthermore, the observed case of young switching broods suggests that they may prefer superior parents and in this way optimize their chances of survival. Because stray chicks and adults act simultaneously seeking adoption, there is no way to know whether the observed adopting better parents (more vigilant and protective than non-adopters) take the initiative in adoption or are chosen by the stray chicks, and only the relationship between better quality males and adoption remains.

The increased brood size after adoption and the fact that adopted chicks are usually younger and thus more vulnerable to predation than the offspring (Codenotti 1995) could suggest exploitation of the adoptees through increased vigilance (due to increased brood size) or by diluting the risk of predation (Hamilton 1971, Pierotti 1988, Riedman 1982) or even redirecting predation towards the more vulnerable foster young. On the contrary, because genetic young in non-adopting broods were not found to do worse than those in adopting broods and, within the latter, adopted young survive in greater proportion than the offspring, we must conclude that it is the adoptees who benefit from adoption.

In precocial species such as the Geater Rhea, whose chicks feed themselves and the adults only guard them, the asymmetry between the low cost to the adult and great benefit to the offspring (Pierotti 1988) probably determines the outcome of the intergenerational conflict towards the success of stray chicks attaining adoption.

Concerning other potential interests for adults, the function of adoption helping to gain reproductive experience (Riedman 1982) is not supported by our observations on Greater Rhea, as adopting males were adults sufficiently skilled and successful as brood leaders.

In the Anatidae, dominance rank on the wintering grounds is apparently determined by the size of the family unit (Black and Owen 1989, Gregoire and Ankney 1990, Lamprecht 1986). Taking advantage of this effect by artificially increasing the size of the family through adoption, adult Lesser Snow Goose (*Chen caerulescens*; Williams 1994) and Barnacle Goose (*Branta leucopsis*; L. Bruinzeel, pers. comm.) increase their dominance rank such that they could compete more successfully for limited food resources. In a similar way, the increased size of adopting broods in the Greater Rhea may have an effect on the dominance rank of adopting

males in the winter flocks, since the male-chick units aparently form the core of these large aggregations (Bruning 1974, Codenotti 1995). In the context of mate choice, it could be that by integrating into the winter flocks (composed of young and adults of both sexes) with their larger broods, adopting males might be providing the females with a sign (family size) of their high quality as parents.

In any case, more information is needed concerning frequency of adoptions in relation to brood density in natural and transformed habitats, because the adoptions are apparently not rare in Greater Rheas living in non-agricultural areas (on the pampas of Argentina, Bruning 1974). Information concerning kinship and social relations between adopting males and those losing young from their broods may also throw light on this topic.

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