

ALLOPARENTAL BEHAVIOR IN THREE NEOTROPICAL GREBES

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ABSTRACT.- Alloparental behavior includes a wide range of situations, from occasional fostering to adoption. It is usually the result of brood parasitism, brood adoption or brood mixing, but also due to nest switching. Interspecific alloparental behaviors are less widespread, but there are no key differences in mechanism of underlying behaviors. Some South American grebes are found sympatrically, and some of them usually reproduce on mixed colonies. Here we describe different conspecific and interspecific alloparental behaviors involving Silvery Grebe (*Podiceps occipitalis*), White-tufted Grebe (*Rollandia rolland*) and the critically endangered Hooded Grebe (*Podiceps gallardoi*). We discuss the implications of temporary adoption and potentially "true" adoption, in particular for Hooded Grebes. Our observations show that alloparental behavior is possibly widespread among Neotropical grebes, and in the case of the Hooded Grebe we hypothesize that alloparental intraspecific feeding of non-related juveniles prior to migration could help to increase juvenile survival.

KEYWORDS: *adoption, alloparental care, creches, Hooded Grebe, Neotropical grebes, Podiceps gallardoi.*

RESUMEN.- CUIDADO ALOPARENTAL EN TRES MACAES NEOTROPICALES. El comportamiento alopARENTAL incluye una amplia gama de situaciones, desde el cuidado ocasional hasta la adopción. Por lo general, esto sucede como resultado del parasitismo de cría, la adopción o la mezcla de crías, pero también debido al cambio de nido. Los comportamientos alopARENTALES interespecíficos están menos extendidos, pero no existen diferencias clave en el mecanismo de los comportamientos subyacentes. Algunos macaes sudamericanos son simpátricos, y generalmente se reproducen en colonias mixtas. Aquí describimos diferentes comportamientos alopARENTALES conspecíficos e interespecíficos que involucran al Macá Plateado (*Podiceps occipitalis*), el Macá Cara Blanca (*Rollandia rolland*) y el críticamente amenazado Macá Tobiano (*Podiceps gallardoi*). Discutimos las implicancias de la adopción temporal y de la adopción "real", en particular en el Macá Tobiano. Nuestras observaciones muestran que el comportamiento alopARENTAL está posiblemente extendido entre los macaes neotropicales, y en el caso del Macá Tobiano, planteamos la hipótesis que la alimentación intraespecífica a juveniles no emparentados antes de la migración podría ayudar a aumentar la supervivencia de estos juveniles.

PALABRAS CLAVE: *adopción, cuidado alopARENTAL, creches, Macá Tobiano, macaes neotropicales, Podiceps gallardoi.*

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Alloparental behavior (i.e. providing parental care towards non-descendant young) includes a wide range of situations, from occasional fostering to adoption, which can be considered an extreme case of alloparental care (Riedman 1982). Alloparental care has been explained with different non-adaptive hypothesis, from simple parental mistakes in recognition of their own young, to failed breeders unable to resist the demand of parental care of unrelated young due to residual reproductive hormones, or brood amalgamation in successful reproducers (Avital et al. 1998). Alloparental care was proposed as a way to gain parental practice by caring for an alien young

(Riedman 1982). In regards to adoption, although it is relatively frequent among birds and mammals (Avital et al. 1998), its occurrence is difficult to explain in terms of evolutionary theory (Riedman 1982).

In most cases, alloparental care is the result of brood parasitism, brood adoption or brood mixing. Brood parasitism occurs almost exclusively in altricial species (Davies 2020), and brood adoption and brood mixing occurs more frequently in precocial or semi-precocial species (Anctil and Franke 2013). Alloparental care can also be the result of nest switching (i.e. young birds which actively abandon their

natal nests to seek temporary or full adoption by foster parents). Nest switching has been reported in semi-precocial species of colonial seabirds such as gulls and terns, but it also occurs in fledglings of altricial species such as raptors, egrets and herons (Redondo et al. 1995, Anctil and Franke 2013). Nest switching in colonial seabirds appears to be more important to increase the rate of chick survival attacks from conspecific than to increase food provision (Kazama et al. 2012). Another important alloparental behavior in many groups of birds, such as flamingoes and penguins, is brood amalgamation, which may range from true amalgamation (without differentiation of own or alien young by adults) to “creche” amalgamation (parents still look for their own chicks, although occasional feeding of alien chicks may happen) (Lengyel 2001).

Interspecific alloparental behaviors are less widespread, but there are no key differences in mechanism of underlying behaviors (Oliveira and Bshary 2021). The most common interspecific alloparental behaviour is brood parasitism, which has been recorded in 109 species to date (Mann 2017). Although not as common as brood parasitism, adoption is a frequent alloparental behavior among different groups of birds, especially in those with precocial and semi-precocial chicks, however it is not restricted to those groups (Avital et al. 1998). Another frequent behavior is interspecific feeding (Shy 1982), which has been recorded in up to 107 different species, mostly associated with males feeding nearby loud chicks (Harmáčková 2021).

Grebes (Podicipediformes) are a homogeneous group of waterbirds, adapted to spend their entire lifecycle in the water. They build their nests mostly on floating platforms and almost half of the extant species tend to breed in colonies (Fjeldså 2004). Some grebe species reproduce in loose colonies within large lakes, while others tend to build tight colonies on small lakes, with a high concentration of nests (Fjeldså 1986, 2004, Roesler 2016). Although some interspecific interaction between neighboring nesting individuals has been mentioned, the only studied alloparental behavior on grebes was intraspecific brood parasitism, which occurs with a rather high frequency in Eared Grebes (*Podiceps nigricollis*) (Lyon and Everding 1996). All grebes have semi-precocial chicks and both parents participate in incubation and food provisioning (Fjeldså 2004). In some grebe species, mainly those that feed on invertebrates, providing food to their young might have a high energetic

cost (Roesler 2016) and therefore, alloparental care should be negatively selected unless the cost-benefit ratio is small enough to increase the chances of survival of ‘cooperative’ behaviors.

In southern South America some grebe species are found sympatrically inhabiting different types of freshwater environments, and some of them usually reproduce in mixed colonies, like the Silvery Grebe (*Podiceps occipitalis*) (SG) and the White-tufted Grebe (*Rollandia rolland*) (WTG) in the Argentinean Pampas (Burger 1974), and the SG and the Hooded Grebe (*P. gallardoi*) (HG; Fig. 1) in the highland plateaus of Austral Patagonia (Fjeldså 1986). Here we describe different conspecific and interspecific alloparental behaviors involving SG, WTG and HG and discuss the implications of temporary adoption and potentially ‘true’ adoption on the breeding biology of these species, in particular on the critically endangered HG.

METHODS

Fieldwork was conducted in two areas, in lakes of Austral Patagonia, at the highland plateaus of western Santa Cruz Province (46°42’S-50°29’S and 71°26’-72°24’W), and in lakes in the southern Pampas, in southwestern Buenos Aires Province (37°37’S, 62°49’W). Lakes in the Patagonian highland plateau are mid-size (5-100 ha), shallow (3-20 m deep) lakes of crystal-clear water, with a single macrophyte species, water milfoil (*Myriophyllum quitense*), which HG and SG use to build their nests. These two grebe species are the only ones reproducing there. Pampas’ lakes are also shallow (1-10 m deep), and they are covered by a more complex plant community, including some species of reeds, mostly *Schoenoplectus californicus*. There are four species of grebes that reproduce in that habitat: SG, WTG, Great (*Podiceps major*) and Pied-billed Grebes (*Podilymbus podiceps*).

During the breeding season (December to April) 2009-2010 to 2016-2017 we monitored 61 colonies of HG accomplishing a total of 1025 days of observation. Of the 61 colonies, 27 were ‘mixed’ colonies with HG and SG. Colony formation was mostly simultaneous, and thus the complete reproductive cycle was essentially simultaneous, with both species reaching chick stage at the same time. Not all the successful colonies were monitored during the complete breeding cycle, but 15 of them were monitored from the time the eggs were laid until the juveniles left the lakes.

In addition, in January and October 2016 we monitored eight lakes with colonies of SG in Buenos Aires province. During this period we conducted two visits of four days each. All lakes had SG and WTG breeding at the same time. The later species usually breeds nearby other species, including SG, but they tend to build their nests solitarily, away from other nesting pairs. During both visits (January and October) nests, chicks and juveniles of both species were detected in at least one of the lakes.

RESULTS

Intraspecific alloparental behavior

In the Hooded Grebe colonies monitored until chick fledging, we detected that chicks between 35-45 days old gathered together generating a post-fledging brood amalgamation. During this period, in all monitored colonies, HG chicks begged to adults and received alloparental feeding. Although the relationship between chicks and adults was unknown, each observed adult fed more than one chick (in some cases up to four chicks in less than 10 minutes) and therefore some of the feedings were directed to unrelated chicks, as HG has only one chick. The feeding occurred upon requesting of food. Chicks beg for food for short periods until adults move away. This period of chicks begging to random adults and receiving alloparental feeding lasted for at least three weeks after emancipation, and in all cases, adults tended to respond in

a non-aggressive way, feeding a few times different young and moving away from the group of chicks.

In addition to these cases of alloparental care after chick fledging, we observed three cases of alloparental care while chicks were still receiving parental care from their parents. On the 31st of January 2017 on LA4 “Mauricio Rumboll” Lake (46°44’14”S, 71°31’51”W) at Buenos Aires Plateau, Santa Cruz, we detected a pair of HG that was acting like they had a chick, but after close observation we confirmed that they did not have one (both were diving, and no chick fell of their backs). One bird in the pair arose from its dive with food and looked around as if trying to find a chick to feed and then the other individual did the same. About 30 minutes later we noticed a second pair that exhibited the same behavior (the first pair was still in sight). One individual took food to the other bird’s back and tried to feed a “phantom” chick (a chick that should have been on the back of the other adult), and shortly after the individual who would have had the chick sitting on its back turned its head around and tried to feed a chick that was not there. Minutes later, another pair passed close to this second pair and one of the adults shook two chicks off its back. The parents of the two chicks began diving for food, and in the middle of the confusion, the pair with the “phantom” chick quickly swam towards one of the chicks that was not being fed at that moment and tried to feed it. Between diving and feeding the two chicks, the real parents attempted to chase away the ‘phantom chick’ pair, who returned multiple ti-

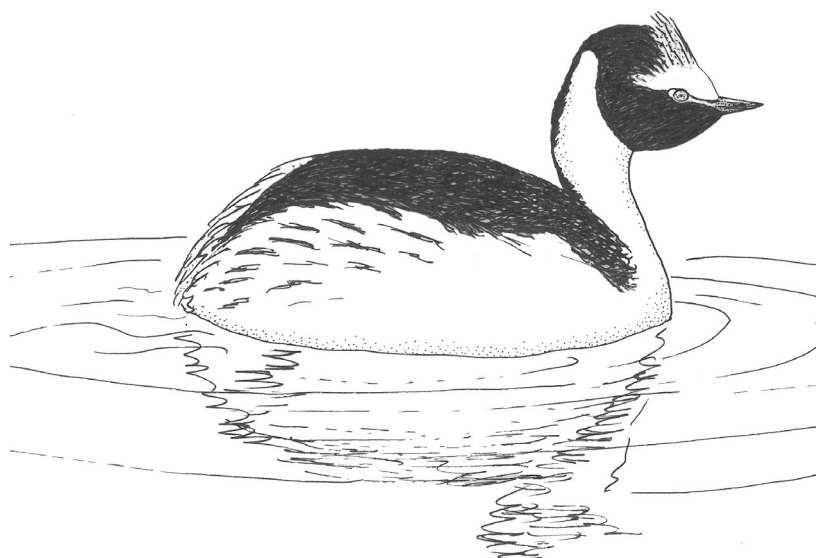


Figura 1. Illustration of an adult Hooded Grebe (*Podiceps gallardoi*) based on a wild individual at El Cervecero Lake at Buenos Aires Lake Plateau. Ilustración: Pagano L.

mes trying to feed one of the two freely swimming chicks. The chicks seemed somewhat reluctant to take food from the 'phantom chick' pair, but on one occasion they appeared to give in, turning toward one member of the 'phantom chick' pair who had food and opening its mouth wide.

On February 1st, 2017, at LA4 Lake we witnessed a HG pair feeding three chicks at once. All nests at that colony were monitored and none of them had more than the typical 2 eggs. One of the chicks was on one adult's back (chick 'A') and the other two were in the water (chicks 'B' and 'C'), with the second adult diving and foraging. During the first 45 seconds the foraging adult either fed or attempted to feed all three chicks, but shortly thereafter all three chicks were swimming freely, the two adults were diving and feeding the three chicks. Three minutes later, the adult who had just fed chick 'A' (chick that was originally on one adult's back) dived to forage and the other adult, who was feeding chicks 'B' and 'C', advanced on 'chick A' and aggressively chased it away. Then chick 'A' swam quickly in the opposite direction. A few seconds later, after both adults dove again, chick 'A' began to swim back towards the other chicks ('B' and 'C') but it kept its distance and both adults began to ignore it. A minute and a half later chick 'A' was at some distance from the pair and the other two chicks ('B' and 'C'), when a third adult popped up and swam directly to it and fed chick 'A'. Interestingly, one of the other two chicks ('C') swam toward this third adult also, as if expecting to be fed. At that point, the original pair were feeding the other two chicks ('B' and 'C'). About 30 seconds later the third adult popped up and started swimming away being followed by chick 'A', who climbed on the third adult's back, swimming off together.

Lastly, on 1 February 2017 at LA4 Lake two pairs (four adults) were fighting over a single chick. One of the pairs was probably the first pair with the 'phantom chick', mentioned above. It was very difficult to separate the two pairs as they seemed to be attacking each other at different times, even members of what appeared to be a pair attacking each other. The chick just swam around trying not to get injured. After over nine minutes of aggressive behavior two adults seemed to claim the chick, and one brought it food. About 20 minutes after the fight, the 'phantom chick' pair was foraging and were again attempting to bring food to a chick that was not there (the 'phantom'), but they were also attempting to deliver food to the chick that they had just been fighting over that was at that

moment riding on the back of its apparent real parent. Later, in the same general area of the lake where this fight occurred, a dead chick was found floating (our interpretation is that this was the former chick of the 'phantom' chick pair).

Interspecific alloparental behavior

We detected two events of adoption involving different grebe species. The first event was on a 4 hectare lake in Buenos Aires Province, where there were 89 adults of SG and 70 adults of WTG. In that lake there was a highly non-synchronic colony of WTG, with five active nests, another four pairs with six chicks and another pair with one independent juvenile. In addition, there were 17 pairs of SG with 18 chicks. The alloparental care event was observed on February 26th, 2016, when an adult WTG fed for a minimum of two hours a 12-15 days old SG chick.

The other interspecific event was recorded on 12 February 2016 in BA90 Lake (46°49'42"S, 70°56'10"W) at Buenos Aires Lake Plateau, Santa Cruz Province. At that lake there were a total of 20 HG adults, six pairs with chicks (one chick per pair, all approximately 3 weeks old), another 8 independent individuals (unpaired and without chicks), and a single *c.* 20-25 days-old chick without any identifiable parent. At the same lake there were 31 SG adults, 15 pairs with one chick per pair (all approximately 3 weeks old), and an unpaired single adult. The single SG adult fed during a minimum of 30 minutes (time we were present at the lake) the lonely HG chick. The behavior of the chick during the time that the observation lasted was "typical" compared to the other chicks that were with their parents (of the same species), begging as soon as the adult emerged and waiting quietly during the periods when the adult was underwater. On successive visits the lonely chick was observed alone, feeding by himself.

DISCUSSION

Our observations showed that alloparental care occurs within some species of the Podicipedidae family. Among grebes there were no reported cases of alloparenting behavior, although there was one indirect mention of this behavior in European species (Dennis 1973). We found that intraspecific alloparental feeding is very common in the Hooded Grebe as it was observed at every monitored successful colony. Also, we observed two cases of interspecific allopa-

rental care, one between WTG and SG and the other between SG and HG.

Intraspecific alloparental feeding behavior in HG happened during the last part of the breeding season (March-April), just before the autumn migration. At that particular moment juveniles are already independent, as they are no longer associated with their parents, congregating in groups (Roesler 2016). During this period, juveniles beg for food to random adults that swim by and adults feed some of those juveniles.

Riedman (1982) proposed that full-grown juvenile fostering would be understandable from an evolutionary perspective in a species with an extremely low reproductive success rate, for which feeding alien chicks at a critical period may increase the possibility of survival of genetically related chicks. The HG has the lowest reproductive rate in the family, with 0.3-0.6 chicks per pair per year (Roesler et al. 2016). The time-span needed for HG to raise a chick is about 45-55 days, and both parents are fully involved with feeding, with an average of over 2500 prey-items per day (Roesler 2016). After chick fledging, adults that bred successfully remain in the lake feeding themselves before the autumn migration while adults whose nests or chicks failed, abandon the colony (Roesler 2016). Thus, most individuals present in the lakes before autumn migration are successful adults (or pairs that lost their chicks at the end of the reproductive cycle). Therefore, it is likely that adults feeding random, independent, juveniles are, in some cases, feeding their own chicks, and thus increasing their chances of survival during migration. Thus, this apparent 'altruistic' behavior could be maintained in HG provided that the benefits the parents receive by increasing the survival of their own chicks are higher than the costs they pay in terms of decreasing their own survival by feeding unrelated chicks.

The fights over the possession of the chicks described above are probably due to the motivational state of reproductive individuals that recently had lost their chicks. The observation of a recently dead chick in proximity of the 'phantom pair' is consistent with this interpretation. This motivational state of providing parental care is what may stimulate adults to attempt to 'steal' chicks.

The two cases of interspecific alloparental behavior observed involved chicks of about two-three weeks of age (about halfway to becoming independent).

Therefore, considering the chicks' age, this could also be a parental hormone-driven behavior, without considering if those chicks belonged to the same species or not. These cases seem to be of low frequency, at least within SG and HG's mixed colonies, since we only detected the interspecific behavior on one occasion after monitoring 27 mixed colonies. The event detected between WTG and SG in only four colonies might indicate that the cross-fostering behavior is more common within WTG, but it could also be an exceptional event.

As mentioned above, it is not easy to find a direct connection between alloparental behavior and natural selection (Riedman 1982). However, alloparental behavior tends to be rather frequent among many species, including birds (Shy 1982). However, not all alloparental behaviors are similar in terms of the energetic cost for the alloparents, and adoption among certain groups of birds seems much more demanding than in others, especially in semi-precocial species (Ancil and Franke 2013), in which nest-switching is not an option, since the chicks abandon the nests few minutes after hatching. In waterbirds, with precocial chicks, adoption has been mentioned (Abraham 1978), and a similar event was observed between an Upland Goose (*Chloephaga picta*) and a Flying Steamer Duck (*Tachyeres patachonicus*) in the study area in Santa Cruz Province (Roesler and Fasola, unpubl. data). However, in this case, like in Ostriches and Rheas, parental effort was restricted only to brood protection from predators, since the chicks feed by themselves, and the evolutionary advantage of this would be to reduce the chances of a complete loss of the brood by splitting the offspring among different groups (Avital et al. 1998).

Our observations show that alloparental behavior is widespread among grebes, and in the case of the critically endangered HG it seems that the alloparental intraspecific feeding of random juveniles prior to migration could help to increase juvenile survival at the time of migration. This behavior may be important for some conservation strategies such as *ex situ* rearing, since it may lead to the decision of where and when hand-reared juveniles should be released.

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