

Aggression by adult South American Terns toward conspecific chicks

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ABSTRACT. Infanticide and nonfatal aggression by adults toward unfamiliar chicks have been widely reported in colonial birds, and can be an important cause of chick mortality. We studied intraspecific aggression by adults toward chicks at a South American Tern (*Sterna hirundinacea*) colony in Patagonia, Argentina, during 2005 to characterize this behavior, evaluate its relationship with nesting density, chick age and microhabitat characteristics, and assess its effect on breeding success. Of 111 chicks in the study area, 45% were attacked at least once. Chicks older than 9 d posthatching were more likely to be attacked than younger chicks, and unattended chicks were more likely to be attacked than guarded chicks (88 vs. 12%). Chicks were also attacked more often when in their own territories (76% of cases), but were less likely to be attacked in territories with more vegetation cover and high-quality shelters (i.e., vegetation with characteristics that prevented adults from reaching chicks). The number of aggression events was not related to nest density. At least 8% of the chicks in our study area died as a result of adult intraspecific aggression. Our results indicate that intraspecific aggression by adult South American Terns toward chicks is relatively common in the Punta Loma colony and should not be underestimated as a factor affecting their breeding success.

RESUMEN. Agresión intraespecífica de adultos a polluelos de *Sterna hirundinacea*

El infanticidio y la agresión no-fatal de adultos a pichones, que no son sus hijos, ha sido ampliamente informado en aves coloniales y puede ser una causa de mortalidad significativa. Se estudio la agresión intraespecífica de adultos a polluelos de *Sterna hirundinacea* en una colonia localizada en Patagonia, Argentina. El trabajo se llevó a cabo durante el 2005 para caracterizar dicha conducta, evaluar su relación con la densidad de nidos, edad de los polluelos, características del microhábitat y finalmente determinar el efecto en el éxito reproductivo. Un 45% (de 111) de los polluelos en la colonia fueron al menos atacados una vez. La proporción de ataques fue mayor en polluelos mayores a nueve días que en los de menor edad y resultó más alta en polluelos que no eran atendidos que en aquellos atendidos por adultos (88 vs 12%). La proporción de ataques fue mayor cuando los polluelos se encontraban en sus territorios (76% de los casos). El número de ataques fue menor en territorios con mayor cobertura de vegetación y en territorios con refugios de alta calidad (ej. vegetación que evitaba que un adulto alcanzara al polluelo) para los polluelos. El número de agresiones no estuvo relacionada con la densidad de los nidos. Al menos un 8% de los 111 polluelos murieron como resultado de agresiones intraespecíficas. Nuestros resultados indican que la agresión intraespecífica de adultos a polluelos de es una conducta común, al menos en la colonia estudiada en Punta Loma y que no debe subestimarse como factor que afecta el éxito de anidamiento.

Key words: Argentina, breeding success, infanticide, intraspecific aggression, *Sterna hirundinacea*

Most seabirds breed colonially, often at high nesting densities (Lack 1968, Coulson 2002) that may increase the chances of aggression between neighboring birds (Wittenberger and Hunt 1985). Intraspecific aggression has been reported between breeding adults, as well as between adults and unfamiliar conspecific chicks in several colonial species (Hunt and McLoon

1975, Quinn et al. 1994, Hill et al. 1997, Ramos 2003, Le Bohec et al. 2005). Several studies, particularly of semi-precocial seabirds, have revealed the regular occurrence of attacks on chicks by conspecific adults that often result in offspring mortality (Mock 1984, Wittenberger and Hunt 1985, Quinn et al. 1994, Ramos 2003).

Infanticide and aggression by adults toward unfamiliar chicks have been reported in different ecological contexts (Mock 1984). Among colonial birds, such behavior generally occurs

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when chicks enter neighboring territories (Hunt and Hunt 1976, Graves and Whiten 1980) when searching for food or shelter or in response to human disturbance (Feare 1976, Hunt and Hunt 1976, Burger and Gochfeld 1991, Gochfeld et al. 1998). Attacks of conspecific chicks by adults may represent an adaptation to avoid adoption and feeding of unfamiliar chicks (Ashmole 1963, Hunt and McLoon 1975, Feare 1976, Pierotti and Murphy 1987, Quinn et al. 1994). Although most studies of semi-precocial seabirds indicate that adult aggression occurs when chicks enter foreign territories (Hunt and McLoon 1975, Mock 1984, Quinn et al. 1994), recent studies of Roseate Terns (*Sterna dougallii*) indicate that adults may also attack chicks in their own territories (Gochfeld et al. 1998, Ramos 2003). Ramos (2003) proposed that high nest densities, open habitat, and parental absence for long periods contributed to such behavior. Although intraspecific aggression has been reported in several other species of terns (Feare 1976, Gauzer 1981, Burger and Gochfeld 1991, Gochfeld et al. 1998, Cuthbert and Wires 1999), no one to date has attempted to quantify the possible role of these factors in such aggression.

South American Terns (*Sterna hirundinacea*) are endemic to South America, breeding from the coasts of southern Peru and central Brazil to Tierra del Fuego, Argentina, including the Malvinas Islands (Gochfeld and Burger 1996, Yorio 2005). Preliminary observations of these terns in a breeding colony located at the Punta Loma Protected Area in Argentine northern Patagonia revealed the regular occurrence of aggression toward chicks, but the characteristics and magnitude of this aggression were unknown. Our objectives were to: (1) examine the attack behavior of adults and the defense behavior of chicks or their parents; (2) determine the possible effects of nest density, parent attendance, chick age, and microhabitat characteristics on aggressive behavior; and (3) quantify chick mortality resulting from conspecific aggression and its effect on breeding success.

METHODS

Our study was conducted during the 2005 breeding season at a tern colony at the Punta Loma Protected Area (42°49'S, 64°28'W), Chubut, Argentina. The colony of about 3200

nests (A. Gatto, unpubl. data) was located along the coast at the top of sedimentary cliffs. Nests were distributed in several patches defined by physiognomic features of the nesting substrate, especially cliff faces broken by small crags. Vegetation consisted of low bushes, mainly *Suaeda divaricata*, *Lycium chilense*, and *Atriplex lampa*. Given the susceptibility of terns to human disturbance, observations were conducted with binoculars (8 × 40) from a blind erected at the periphery of the colony. Observations started no sooner than 10 min after entering the blind to minimize possible bias due to changes in behavior resulting from our approach. We selected 111 nests adjacent to the blind for study. No adults, chicks, or nests were marked. The limited mobility of chicks and variability in plumage facilitated assignment to specific territories. All focal nests were checked every 2 d from 10 December until chicks fledged, except during peak hatching when nests were checked daily. During each nest check, the numbers of eggs or chicks were recorded. For nests checked every 2 d during hatching, hatching date was assumed to be the day after the egg was last seen. Chicks not recorded in their nest after three consecutive nest checks were assumed dead, except those older than 27 d posthatching when young start to fledge (Scolaro et al. 1996).

To analyze intraspecific aggression, observations were conducted during observation periods lasting at least 2 h for a total of 37 h on 11 nonconsecutive days from 20 December 2005 to 10 January 2006. Observations were conducted throughout the day and during different stages of the tidal cycle and various weather conditions. Aggression was defined as an adult making physical contact with an unfamiliar chick. An aggression event included all behavior from when an adult first made physical contact with a chick and continuing up to 15 sec after the chick stopped being attacked by the same adult or a different one that joined the interaction. For each aggression event, we recorded: (1) the start and end time, (2) the attacked chick's nest, (3) chick age, with age categorized as either young (chicks ≤9 d old, an age considered critical for chick survival; Scolaro et al. 1996) or old (chicks >9 d old), (4) the aggressive behavior of the attacker, categorized as pecking, grabbing (holding the chick for a few seconds and preventing its movement) and removing (taking a chick in its beak, flying a few meters,

and dropping it), (5) total number of pecks, (6) victim's response to the attack, (7) presence or absence of parents at the nest, (8) territorial identity of the attacker (if the bird was recorded approaching the victim from a territory bordering the victim's nest or from another territory), and (9) distance of the chick from its nest when attacked (estimated using chick body size or the adult's head or beak as relative measurement units, transforming these to centimeter using known morphometric measurements).

Territories were defined as the area within a 20-cm radius centered at a nest (equivalent to half the mean nearest neighbor distance in our study area). An attacked chick was considered to be in its nest if it was in the nest scrape, in its territory if outside the nest scrape, but less than 20 cm away, and outside its territory if more than 20 cm from the nest scrape. After each aggression event, chicks were recorded as dead or alive. A chick was considered dead if carried away from its nest and not seen returning to its territory or if it was not seen to move by the end of that day's last observation period.

Nest-site variables were measured at all focal nests after breeding was over (late January), including the percentage of vegetation cover within a 30-cm radius around the nest, nearest neighbor distance, and, if present, shelter quality. Shelters were defined as any structure that provided chicks with protection from an aggressor. Shelters were categorized as either high or low quality, with high quality indicating that shrub size, canopy density, or entrance dimensions prevented adults from reaching a chick. Vegetation cover (ground area covered by vegetation) in territories was classified as no cover (0%), low (up to 30%), or high (over 30%). Nest density was estimated from nearest neighbor distances.

Contingency tables and the χ^2 statistic were used to compare the defense behaviors of chicks in different contexts. Possible differences between age classes in the number of times pecked were tested using the nonparametric Kruskal-Wallis test. Sample sizes differ because we were not always able to determine chick age or monitor all behaviors during an aggression event. The possible relationship between nearest neighbor distance and the number of attacks was analyzed using Spearman rank correlation. Generalized linear models (GLM) with Poisson error structure and log-link function (Crawley 2007) were

used to test the effects of (1) chick age and parent attendance, (2) chick age and type of aggressive behavior, and (3) vegetation cover and shelter quality on the number of chicks attacked. Models were fitted using R software version 2.7.2 (R Development Core Team 2008). Models with all possible combinations of predictor variables were considered, and best models (i.e., best of suitable models) were selected using Akaike's Information Criterion (AIC) and likelihood ratio tests (LRT) (Burnham and Anderson 2002). Means are reported ± 1 SD.

RESULTS

Aggressive behavior and aggressor identity. We observed 199 acts of aggression by adult terns toward unfamiliar chicks. Of 111 chicks in our study area, 51 (46%) were attacked at least once (mean = 1.4 ± 1.7 , range = 0–14). The mean duration of aggression events was 33 ± 43 sec ($N = 74$, range = 2–203 sec). Adult terns attacked chicks by pecking (78%, $N = 170$), grabbing (15%), and removing them (7%). Pecking generally involved several pecks, with a mean number of 4.6 ± 4.5 per event ($N = 186$; range = 1–25). Adults pecked both young and old chicks, but young chicks (mean = 7.5 ± 7.1 pecks, $N = 34$) were pecked more per aggressive event (Kruskal-Wallis test, $H_{1,124} = 5.4$; $P = 0.017$) than were old chicks (mean = 3.8 ± 3.4 pecks, $N = 90$). In 29 cases, the attacking adult(s) alternated behaviors in the same event, grabbing and pecking the chick, whereas, in six cases, the adult pecked and then removed the chick from its territory.

The aggressive behavior of adults varied with chick age (Table 1). The model that best fit these data (GLM test, AIC = 33.6, LRT: $\chi^2_5 = 153.0$, $P < 0.0001$) indicated that the number of chicks

Table 1. Percentage of attacked young and old chicks by conspecific adults using different aggressive behaviors at the South American Tern colony in Punta Loma, Argentina, during the 2005 breeding season (number of attacked chicks in parentheses).

Chick age	Aggressive behavior		
	Pecking	Grabbing	Removing
Young (<9 d old)	80.0 (28)	0.0 (0)	20.0 (7)
Old (> 9 d old)	80.5 (66)	18.3 (15)	1.2 (1)

that were attacked varied with chick age ($c_1^2 = 41.7$, $P < 0.0001$) and adult aggressive behavior ($c_2^2 = 133.6$, $P < 0.0001$). Model parameters indicated that more chicks were attacked by pecking than by other types of aggressive behaviors ($z = 6.6$, $P < 0.0001$) and old chicks were attacked more than young chicks ($z = 4.2$, $P < 0.0001$). In addition, we found an interaction between type of aggressive behavior and chick age ($\chi_1^2 = 19.4$, $P < 0.0001$), with young chicks removed more often, and pecked and grabbed less often than old chicks.

Unattended chicks were attacked more often than attended chicks (88 vs. 12%), but old chicks (>9 d old) were more likely to be left alone than young chicks (≤ 9 d old). The model that best fit these data (GLM test, AIC = 27.1, LRT: $\chi_3^2 = 96.1$, $P < 0.0001$) indicated that the likelihood of chicks being attacked depended on parent attendance ($\chi_1^2 = 61.7$, $P < 0.0001$) and chick age ($\chi_1^2 = 21.2$, $P < 0.0001$). Chicks that were alone were attacked more often than those who were attended ($z = 6.0$, $P < 0.0001$) and old chicks were attacked more often than young chicks ($z = 5.2$, $P < 0.0001$). We also found an interaction between parent attendance and chick age ($\chi_1^2 = 13.2$, $P < 0.0001$), with young attended chicks attacked more than old attended chicks and old, unattended chicks attacked more than young, unattended chicks.

Most attacks (76%) occurred when chicks were in their own territory ($\chi_1^2 = 49.1$, $P < 0.0001$, $N = 184$), and 90% of attacks within territories occurred in nest scrapes. At least 43% of 199 observed aggression events involved adults from territories immediately adjacent to the victim's nest, with 19% by adults from other territories and 38% by unidentified adults. Most attacks by adults from adjacent territories (78%; $N = 86$) were by adults that also had chicks. Five attacks were by subadult birds wandering among the nests and pecking unattended chicks.

Defense behavior of adults and chicks.

We did not observe defense of chicks by parents during any of the 21 attacks initiated when one of the parents was present at the nest. In at least 11 cases, when an aggression event began, the parent left the territory or attacked another neighboring adult while its chick was attacked. During three of 149 events where chicks were unattended at the start of the attack, one of the parents approached the nest and actively defended its offspring either by pecking at the

Table 2. Responses of young and old chicks to adult intraspecific aggression at a South American Tern colony in Punta Loma, Argentina, during the 2005 breeding season.

Chick age	Response behavior ^a		
	Crouching	Moving	Pecking
Young (<9 d old)	45.0 (15)	55.0 (18)	0.0 (0)
Old (>9 d old)	29.0 (25)	46.6 (40)	24.4 (21)

^aPercent responding (number of chicks attacked).

intruder or moving between its chick and the attacker.

Chicks responded to attacks by moving, pecking at the intruder, or crouching until a few seconds after the attack ended, with chicks moving (56%) more often than crouching (31%) or pecking (13%; $\chi_2^2 = 45.2$, $P < 0.0001$, $N = 169$). Chick responses to attacks varied with age ($\chi_2^2 = 10.3$, $P < 0.05$, $N = 119$), with young chicks more often responding by crouching and only old chicks pecking attackers (Table 2). Chicks usually moved away from aggressors when unattended and crouched when a parent was present ($\chi_2^2 = 13.3$, $P = 0.0013$, $N = 151$).

Aggression and microhabitat characteristics. The likelihood of chicks being attacked by adults was influenced by the amount of vegetation cover and the quality of shelter in chick territories (GLM test, AIC = 51.5, LRT: $\chi_3^2 = 101.2$, $P < 0.0001$). The model that best fit these data included a significant effect of shelter quality ($\chi_1^2 = 51.9$, $P < 0.0001$) and vegetation cover ($\chi_2^2 = 49.3$, $P < 0.0001$). Chicks in territories with low-quality shelters were attacked more often than those with high-quality shelter in their territories ($z = 5.6$, $P < 0.001$), and chicks in territories with low vegetation cover were attacked more than those in territories with no cover or high vegetation cover ($z = 4.7$, $P < 0.001$).

Mean nearest neighbor distance was 43 ± 10 cm ($N = 111$; range = 15–80 cm) in our study area, and 53 ± 22 cm ($N = 132$; range = 42–76 cm) for the entire colony. The number of aggression events experienced by chicks was not related to nearest neighbor distance ($r_s = 0.06$; $P = 0.6$).

Aggression and breeding success. A total of 111 chicks hatched from the 109 nests with eggs (mean = 1.01 ± 0.6 per nest), with

two chicks at 18 nests. With one exception, chicks at these 18 nests did not survive more than a week. A three-chick brood was recorded at one nest; two of these chicks were killed due to intraspecific aggression when less than a week old and the remaining chick fledged. Of the 111 chicks, 39% died within a week of hatching and 31% fledged.

At least 9 of 111 chicks (8%) died as a result of adult aggression. Four of these chicks were in single-chick broods, two in two-chick broods, and three in the same three-chick brood. Six deaths resulted from adults using "removing" behavior and three chicks were pecked to death. All removed chicks and one of the chicks pecked to death were young, and the rest were old chicks. Of 34 chicks that fledged, 26% were attacked at least once.

DISCUSSION

Infanticide and nonfatal aggression by adults toward unfamiliar chicks have been widely reported in terns and gulls, and can be a major cause of chick mortality (Hunt and Hunt 1975, Davis and Dunn 1976, Fetterolf 1983, Brown and Morris 1995). Our results show that intraspecific aggression of adult South American Terns toward chicks was common at the Punta Loma colony. In general, adult aggressive behavior toward chicks consisted of repeated pecking, but chicks were sometimes removed from their territories. Similar behavior, with chicks carried in the bill and dropped several meters from nest sites, has been reported during aggressive encounters between Roseate Tern adults and chicks (Ramos 2003).

Young chicks were attacked less frequently than old chicks because, unlike old chicks, young chicks were generally guarded by one of their parents. In most larids, at least one parent remains at the nest site during the first days after hatching when chicks are more vulnerable (Burger and Gochfeld 1991). However, we observed no defense behavior in 21 cases where at least one parent was present at the nest at the time of an attack. As reported by Ramos (2003) for Roseate Terns, aggression by conspecific adults usually involved unattended chicks. Although more aggression events were directed toward old chicks, attacks of young chicks were more intense and only young chicks were carried from their territories. Thus, young

chicks appear to be more vulnerable to intraspecific adult aggression.

In general, studies of larids have revealed that both fatal and nonfatal aggression occurs when chicks move from their nest sites and enter the territory of the aggressor (Hunt and McLoon 1975, Feare 1976, Mock 1984, Pierotti and Murphy 1987, Quinn et al. 1994). In contrast to most previous studies, adult aggression toward chicks in our study occurred primarily within the chick's territory. This behavior has been only reported in Roseate Terns, both in North America (Gochfeld et al. 1998) and the Seychelles Islands, and, at the latter location, in similar proportions to that observed in our study (Ramos 2003). The cause of this aggression within the territory is not clear, but Ramos (2003) argued that removing chicks from their territory could reduce the risk of adopting or feeding unfamiliar offspring. Unfortunately, our data cannot confirm or refute this hypothesis, so additional study is needed to evaluate the relationship between aggression and food availability and the occurrence of adoption behavior by South American Terns.

South American Terns at Punta Loma nest in a physically heterogeneous habitat, with vegetation that offers protection for chicks. The presence of vegetation cover is a key factor in the selection of nesting habitat for many species, and several studies of seabirds have shown that cover affects breeding success by providing protection against inclement weather conditions and predation (Calladine 1997, Stokes and Boersma 1998, García Borboroglu and Yorio 2004). Vegetation cover can also reduce intraspecific aggression by decreasing the visibility of conspecifics (Burger 1977, Cezilly and Quenette 1988, Bukacinska and Bukacinski 1993). Although we found that the number of intraspecific attacks was lower in territories with greater vegetation cover, it is not clear why few chicks were attacked in territories with no cover. In addition, the number of attacks in our study was lower in territories with shelters that allowed chicks to hide deep within the vegetation where they could not be reached by larger adults. Thus, high-quality shelters in territories appear to provide breeding South American Terns with protection against intraspecific aggression.

High nesting densities may result in increased aggression between neighboring birds (Butler and Trivelpiece 1981, Butler and Janes-Butler 1982), including increased adult aggression

toward chicks and infanticide (Mock 1984, Hill et al. 1997). Ramos (2003), for example, argued that the high nesting density at his study site may have been a factor in the aggressive behavior of adult Roseate Terns toward chicks. However, we found no relationship between nest density and aggression by adult South American Terns toward conspecific chicks.

Our results indicate that aggression by adult South American Terns may result in chick mortality, with 8% of the chicks hatched in our study area killed by conspecific adults. However, this represents a minimum estimate because the consequences of repeated pecking on chicks, particularly young ones, on days following the attack are unknown and some chick mortality resulting from attacks could have occurred outside our observation periods. Thus, aggressive behavior of adults toward unfamiliar chicks should not be underestimated as a factor affecting the breeding success of South American Terns, at least in our study area.

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