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Kleptoparasitism by Brown-hooded Gulls and Grey-hooded Gulls on American Oystercatchers

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Abstract.—This study describes qualitatively and quantitatively the kleptoparasitic behavior of the Brown-hooded Gull (*Larus maculipennis*) and Grey-hooded Gull (*Larus cirrocephalus*) on the American Oystercatcher (*Haematopus palliatus*), and considers the influence of environmental variables on the occurrence and success of the kleptoparasitism. Focal and scan samplings were performed, recording a total of 358 kleptoparasitic attempts. The overall occurrence rate was 1.2 ± 1.3 attempts per 5 min., of which 42% of attempts were successful. All kleptoparasitic attempts were performed when oystercatchers were feeding on Stout Razor Clams (*Tagellus plebeius*). Gulls stole food from Oystercatchers by two kleptoparasitic tactics; running (used in 40% of cases) and flying (used in 60% of cases). A significant difference in the rate of success of kleptoparasitism and an increase in the use of flying kleptoparasitism were observed under windy conditions. Gulls showed limited ability to open clams by themselves, and never swallowed whole clams. Kleptoparasitic attacks occurred within three seconds of the clam being ingested by the host, indicating the accurate kleptoparasitic skills of hooded gulls. Possible factors that affected the decisions taken by gulls about when and how to start the robbing behavior are discussed. Features of the kleptoparasitic behavior performed by hooded gulls on oystercatchers provide some relevant questions regarding the "generalist" or "specialist" character of these parasites.

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Key words.—Kleptoparasitism, *Larus*, gulls, Oystercatchers, Mar Chiquita, Argentina.

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Many gull species are kleptoparasites, stealing different kinds of food from several hosts (Furness 1987; Burger 1988; Hesp and Barnard 1989; Burger and Gochfeld 1996). Kleptoparasitism by Brown-hooded Gulls (*Larus maculipennis*; BHG) and Gray-hooded Gulls (*Larus cirrocephalus*; GHG) on the American Oystercatcher (*Haematopus palliatus*) has been reported in Mar Chiquita coastal lagoon (Martínez and Bachmann 1997). Of these two gulls, BHG is the main kleptoparasite, both in abundance of individuals and in occurrence of kleptoparasitic events, while GHG and other gull species such as Olrog's Gull (*Larus atlanticus*) and Kelp Gull (*Larus dominicanus*) represent a small fraction of the total events reported (Bachmann 1995; M. Favero unpubl. data). The kleptoparasitic behavior of hooded gulls reported in the study area was only performed during the winter, when the American Oystercatcher fed mainly on Stout Razor Clams (*Tagellus plebeius*), a common bivalve in estuaries of the regions. Between March and early September, clams constituted the main prey of American Oystercatchers, while during the austral summer the diet shifted mainly to females of the crab species *Cyrtograpsus angulatus* (Bachmann 1995).

It has been reported that weather conditions and/or tidal height can affect the outcome of kleptoparasitic attempts (Hackl and Burger 1988). In the Mar Chiquita coastal lagoon, water level changed according to tidal influence and/or water contributed from rivers (see Fasano *et al.* 1982 for details). This variation also affects the exposure of clams of different sizes and densities (Iribarne *et al.* 1998), changing the clam sizes available to predators such as Oystercatchers, and thus affecting the profitability of clam stealing by hooded gulls.

This study describes qualitatively and quantitatively the kleptoparasitic behavior of BHG and GHG on the American Oystercatcher, specially considering the influence of environmental variables on the occurrence and success of kleptoparasitism.

METHODS

This study was carried out in Mar Chiquita coastal lagoon, Buenos Aires Province, Argentina (37°46'S, 57°27'W). Weekly observations were carried out between October and December 1998, and March and November 1999. Focal and scan samplings were performed following Altmann (1974) and Martin and Bateson (1993). The date, time, tidal height and wind strength were recorded immediately before each period of observations. Wind strength was scaled in four classes (0 = calm; 1 = light wind < 10 $km.h^{-1}$; 2 = moderate 10–30 $km.h^{-1}$; 3 = strong winds > 30 $km.h^{-1}$). Tidal height was grouped into classes according to the degree of exposition of the shore (0 = very low [spring tide]; 1 = low [neap tide]; 2 = intermediate; 3 = high).

Scan samplings were used to estimate the abundance and kleptoparasite-host ratio. Focal samplings were conducted on individuals randomly selected, using 10× binoculars and 12-36× spotting scopes. Samplings were made on both kleptoparasites and hosts. In every focal sampling, all activities performed by birds were recorded. The minimum and maximum duration of each sample was 5 and 10 min., respectively, totaling 30 h. of observation and 358 kleptoparasitic attempts recorded. All results throughout the text and tables are given as means ± one standard deviation.

RESULTS

The most frequently observed ratio between feeding oystercatchers and kleptoparasitic gulls was 1:1 (58% of total cases), being one gull *vs.* one oystercatcher most frequently (53%) (Fig. 1). Other group compositions varied from two gulls with eleven oystercatchers, to four gulls with one oystercatcher. In almost all the observed attempts (99%), kleptoparasitic attacks were performed by one gull independent of the group. Only five attempts (about 1% of observations) were performed by more than one gull at once. While feeding, BHG and GHG spent at least 47% of their time kleptoparasitizing oystercatchers

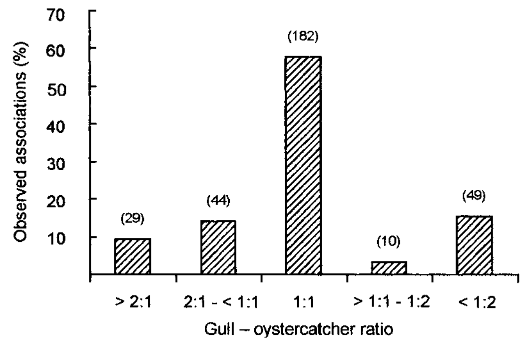

Figure 1. Percentual occurrence of ratios between feeding oystercatchers and kleptoparasitic hooded gulls in Mar Chiquita Lagoon. Sample size in brackets.

(including associations and attacks), and other time was spent searching for food, scavenging and in comfort behavior (Fig. 2).

A total of 358 kleptoparasitic attempts was recorded, showing an overall rate of 1.2 ± 1.3 attempts every 5 min. (all gulls pooled). There was no significant difference between the attack rates by BHG (1.2 ± 1.4 every 5 min.; N = 106) and GHG (0.8 ± 1.1 every 5 min.; N = 39) (U-test Z_1 = 0.87; n.s.). There was also no significant difference in the comparison of success rate in BHG (41.1%; N = 197) and GHG (40.7%; N = 81) (χ^2_1 = 0.001; $P > 0.05$). The overall success rate for all hooded gulls (N = 358) was 41.9%. All kleptoparasitic attempts were performed on oystercatchers that were feeding on clams.

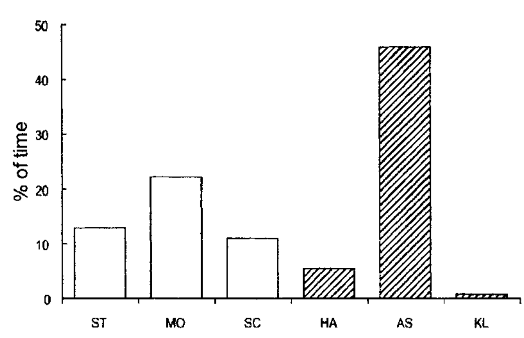

Figure 2. Time budget of main behavioral categories of hooded gulls foraging in Mar Chiquita lagoon, showing the time spent during kleptoparasitic (hatched bars) and non-kleptoparasitic activities (open bars). ST = standing (comfort behavior included), MO = moving (includes walking, swimming and flying), SC = scavenging, HA = handling (kleptoparasitized items), AS = associated with oystercatchers, KL = kleptoparasitic attacks.

Gulls stole food from Oystercatchers by using two kleptoparasitic tactics, which were named as *running* and *flying* kleptoparasitism. In the first, gulls approached their hosts by running from a nearby position, while in the latter one, the gulls flew toward the oystercatchers. *Flying* (60%) was used significantly more often than *running* kleptoparasitism (40%; N = 358) ($\chi^2_1 = 14.4$; $P < 0.001$). *Flying* had a 43.0% (N = 216) success rate, while *running* had an almost identical success rate of 40.1% (N = 142) ($\chi^2_1 = 0.12$; n.s.). The interactions observed during attacks were usually accompanied by calling by the birds involved. In most cases (87%), gulls ate the kleptoparasitized food nearby the place of robbery.

As shown in Table 1, kleptoparasitic rates did not increase significantly with wind strength (Kruskal-Wallis test $H_3 = 1.59$; n.s.). There was a significant increase in the use of *flying* as wind strength increased ($\chi^2_3 = 50.7$; $P < 0.001$). A significant difference in the success rate of kleptoparasitic attempts was observed only in strong winds ($\chi^2_1 = 9.0$; $P < 0.005$) (Fig. 3B). There were no significant differences in the frequency ($H_3 = 3.91$; n.s.) or the success rate ($\chi^2_3 = 0.32$; n.s.) of kleptoparasitism under different tidal heights (Table 1).

Most kleptoparasitic attacks (96% of the cases) occurred within the first three seconds of ingestion of clams by an oystercatcher, after they had opened the valves. Gulls lacked the skills required to open clams; in two cases it was observed that gulls were unable to open stolen clams that had not been opened by oystercatchers. Gulls were never observed swallowing whole clams.

DISCUSSION

The variation in the tactics used by gulls in kleptoparasitic attacks on oystercatchers could be affected by several causes. The decisions taken by gulls as to when and how to start the robbing behavior seems to be affected by one or a combination of the following factors: (1) individual differences in the distance and/or position of the kleptoparasite in relation to the host, (2) individual differences in host's avoidance behavior, (3) individual differences in the kleptoparasite's

Table 1. Kleptoparasitic success and kleptoparasitic rates (attacks every 5 min) of hooded gulls upon Oystercatchers according to wind class and tide height at Mar Chiquita lagoon. See scale references in methods section.

	Kleptoparasitic success (%)				Kleptoparasitic rate (sample size)
	BHG (N = 197)	GHG (N = 81)	UG (N = 80)	Overall (N = 358)	
Wind speed					
0 (N = 93)	41.8	37.5	40.9	40.9	(a)
1 (N = 120)	38.3	40.0	31.6	37.5	0.88 ± 1.08 (50)
2 (N = 92)	36.8	34.3	42.1	37.0	1.27 ± 1.48 (84)
3 (N = 53)	56.5	70.0	65.0	62.2	1.41 ± 1.4 (35)
Tidal height					
0 (N = 112)	40.0	40.0	50.0	41.1	0.82 ± 1.26 (28)
1 (N = 83)	45.9	44.8	40.0	43.4	1.26 ± 0.89 (34)
2 (N = 123)	40.2	40.0	56.3	42.3	1.44 ± 1.57 (40)
3 (N = 40)	50.0	33.3	36.4	40.0	1.02 ± 1.29 (74)

BHG: Brown-hooded Gull, GHG: Grey-hooded Gull, UG: unidentified hooded gulls.
(a) Sample size was too small for independent analysis (class 0 was pooled with class 1).

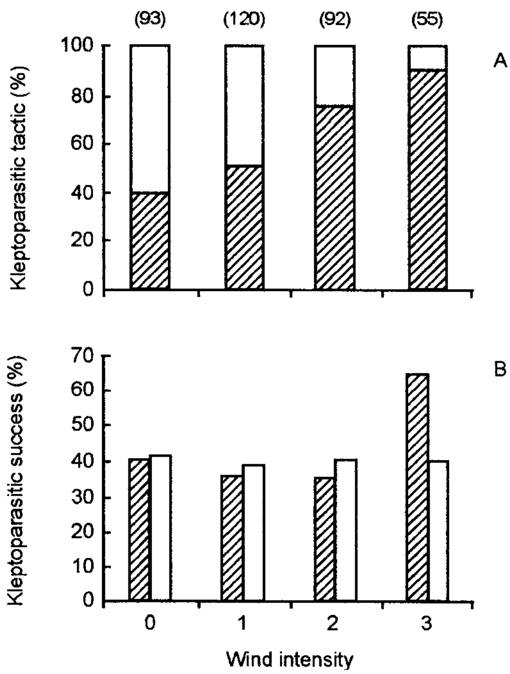

Figure 3. Variation in the use of kleptoparasitic tactics (A) and success (B) according to wind intensities. Hatched bars: flying kleptoparasitism; open bars: running kleptoparasitism. Wind intensity was scaled using four class intervals (0 = calm; 1 = light wind < 10 km.h^{-1}; 2 = moderate 10–30 km.h^{-1}; 3 = strong winds > 30 km.h^{-1}). Sample size in brackets.

skills to perform different tactics, and (4) physical environmental conditions.

According to Bachmann (1995), the kleptoparasitism of BHG and GHG on the American Oystercatcher produced a high reduction in the host's food intake rate. This concurs with the high gull—oystercatcher ratio (Fig. 1), gull concentrations in the area and overall success rate found in this study (42%) which is higher than those reported in the literature. In a review of the kleptoparasitic behavior in seabirds (Furness 1987), the success rates vary from 1% to 85%, with a median of 23%. Moreover, the kleptoparasitic behavior is important in the total time budget of hooded gulls in the study area (see Fig. 2), and winter kleptoparasitism is an important foraging strategy for the gulls in the Mar Chiquita coastal lagoon.

The potential benefits of each kleptoparasitic attempt could be analyzed, as proposed by Thompson (1986), taking into account three factors: the energetic cost of the attack, the chance of success and the energetic reward. During our study, there was a slightly higher tendency to use *flying* (60%) over *running*; and overall success rates were similar under different weather conditions (Fig. 3B). When the wind was strong, it seemed likely that gulls improved their flying maneuverability and speed. It was suggested that the early detection of attacks by hosts could reduce the overall chances of success (e.g., Watt *et al.* 1995; Goss-Gustard *et al.* 1999), so an increase in the flying speed might be an important component of a successful attack. Moreover, strong winds could decrease the energetic costs of flying (see King 1974; Muggas and King 1981), mainly during the take-off and landing. The use of *flying* is strongly associated with strong winds (Fig. 3A). With low or moderate winds, the coexistence of both robbing tactics could result from the interplay between two opposed attributes of *flying*: the relatively higher energetic cost of flying, against the benefit of a fast approach and escape from the host. Despite the fact that under low winds there were no differences in the success rates of *flying* and *running*, the use of the former tactic could imply lower risk of potential injuries due to oystercatcher's defense (facing and running toward the gull).

It has been proposed that interspecific kleptoparasitism developed in some birds as a mechanism to acquire inaccessible prey easily obtained by hosts (see Brockmann and Barnard 1979; Duffy 1980; Furness 1987). In the relationship between hooded gulls and oystercatchers, the inability to open and handle clams is an important factor in the development of kleptoparasitism. The interval between the beginning of the consumption (after opening clams) and the subsequent three seconds is the most profitable timing. On the one hand, it is likely that later attempts to steal clams would bring lower returns because of partial or entire consumption of the prey by the oystercatchers. On the other hand, any clam stolen before the oystercatcher opens it offers no energetic reward since gulls cannot open the valves. This situation was observed in less than 1% of cases, which is evidence of accurate kleptoparasitic skills (i.e. timing) by the hooded gulls.

Clams scavenged by hooded gulls come from prey previously consumed by oystercatchers. It has been suggested that one of the mechanisms by which interspecific kleptoparasitism developed was by the gulls following oystercatchers to take the prey remains (i.e. scavenging) (Brockmann and Barnard 1979). Despite the low return of this carrion (small soft tissue mass per clam), the energetic cost of searching is, at least intuitively, low. Both kleptoparasitism and scavenging were not exclusive activities in hooded gulls, but the former showed up strongly in the gull's time budget, while scavenging seems to be only an occasional behavior.

The features of the kleptoparasitic behavior performed by hooded gulls on oystercatchers raise some relevant questions regarding the "generalist" or "specialist" character of parasites. On the one hand, the behavior of the gulls shows "generalist" attributes, such as the inability to cause food regurgitation in hosts, high impact upon host numbers (at least due to high parasites host ratio; see Bachmann 1995), and the coexistence with other foraging strategies or the use of alternative resources (Favero *et al.* 2001). On the other hand, hooded gulls also show some "specialist" attributes such as the very accurate timing in the kleptoparasitic attack and the high success rates compared to those reported for other specialist kleptoparasites (see Furness 1987). Further studies focused on kleptoparasitic skills and learning abilities in relation to age will allow a better understanding of evolutive processes involved in the kleptoparasitic behavior of hooded gulls during winter in Mar Chiquita.

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