FACTORS AFFECTING KLEPTOPARASITISM BY GULLS IN A MULTI-SPECIES SEABIRD COLONY

GERMÁN OSCAR GARCÍA[1,2,4], MARCO FAVERO[1,2], AND ALDO IVÁN VASSALLO[1,3]

[1]*Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Av. Rivadavia 1917,
C1033AAJ Buenos Aires, Argentina*
[2]*Laboratorio de Vertebrados, Departamento de Biología, Facultad de Ciencias Exactas y Naturales,
Universidad Nacional de Mar del Plata, Funes 3250, B7602AYJ Mar del Plata, Argentina*
[3]*Laboratorio de Ecofisiología, Departamento de Biología, Facultad de Ciencias Exactas y Naturales,
Universidad Nacional de Mar del Plata, Funes 3250, B7602AYJ Mar del Plata, Argentina*

Abstract. Kleptoparasitism is defined as the stealing by one animal of food that has been caught by another. It is a well-known foraging tactic used opportunistically by many seabirds. Our study describes qualitatively and quantitatively kleptoparasitism of gulls on terns and compares the effect of prey quality (prey type and size) and environmental conditions (tide, wind direction and intensity) triggering such behavior. The rate of kleptoparasitism by Kelp Gulls (*Larus dominicanus*) was higher on Royal (*Thalasseus maximus*) than on Cayenne Terns (*T. sandvicensis eurygnatha*). However, the percentage of successful attacks on both species was similar (~42%). We used an information-theoretic approach to determine the relative importance of prey quality and environmental conditions in triggering kleptoparasitism. We found that more valuable prey triggered kleptoparasitism whereas the environmental conditions included in the models didn't affect the rate of such behavior significantly. Our study shows the importance of prey quality in triggering kleptoparasitism and how this behavior can remove an important portion of food brought to the tern colony.

Key words: information-theoretic approach, kleptoparasitism, multi-species colony, Patagonia, seabirds.

Factores que Afectan el Cleptoparasitismo por Gaviotas en una Colonia Multiespecífica de Aves Marinas

Resumen. El comportamiento de cleptoparasitismo es definido como el robo deliberado por un individuo de la comida capturada previamente por algún otro. Este tipo de comportamiento ha sido registrado en diferentes grupos de animales. Sin embargo, las aves, y en especial las aves marinas, son el grupo en el que este comportamiento está más ampliamente reportado en la bibliografía. En este estudio se describe cualitativa y cuantitativamente el comportamiento de cleptoparasitismo de las gaviotas sobre los gaviotines, y además se compara el efecto de la calidad de las presas (tipo y tamaño) y las condiciones ambientales (estado de la marea, dirección e intensidad del viento) como factores desencadenantes de este comportamiento. La tasa de cleptoparasitismo practicado por *Larus dominicanus* fue mayor sobre *Thalasseus maximus* que sobre *T. sandvicensis eurygnatha*. Sin embargo, el porcentaje de éxito de los ataques fue similar en ambas especies (~42%). Se utilizó un enfoque basado en teoría de la información para determinar la importancia relativa de los efectos de los factores tróficos y ambientales sobre el cleptoparasitismo. Nuestros resultados muestran que las presas con mayores retornos energéticos desencadenaron el cleptoparasitismo, mientras que las condiciones ambientales incluidas en los modelos no afectaron de forma significativa la ocurrencia de dicho comportamiento. En este estudio se muestra la importancia de la calidad de las presas como desencadenante del cleptoparasitismo, y cómo este comportamiento puede remover una porción importante del alimento llevado a la colonia de gaviotines.

INTRODUCTION

Kleptoparasitism is defined as the stealing by one animal of food that has been caught by another (i.e., the host; Furness 1987). This behavior has been reported in many species, including marine invertebrates (Iyengar 2004), insects and spiders (Vollrath 1984), fish (Grimm and Klinge 1996), reptiles (Cooper and Perez-Mellado 2003), birds (Brockmann and Barnard 1979), and mammals (Kruuk 1972, Brown et al. 2004).

Observations of birds as kleptoparasites are among the most detailed, and Brockman and Barnard (1979) provided a comprehensive list of observations and notes on various species and kleptoparasitic strategies. Kleptoparasitism is much more common in some groups of birds, especially seabirds,

than in others (Furness 1987). Some birds, such as skuas and jaegers (*Stercorarius* spp.), are primarily kleptoparasites, particularly during the nonbreeding season. Others, such as gulls and terns (Laridae), may kleptoparasitize opportunistically in breeding colonies or in areas where birds congregate for feeding, such as at landfills or behind fishing vessels (Hudson and Furness 1988, Steele and Hockey 1995).

Prey quality, among other ecological conditions, may facilitate kleptoparasitism (Brockmann and Barnard 1979). Several studies have found that kleptoparasitism is more likely when food items are large or rich in energy (Leschack and Hepp 1995, Steele and Hockey et al. 1995, García et al. 2008). If prey is larger the time the host must handle it may be longer, increasing the likelihood of kleptoparasitic attack (García et al. 2008). Additionally, environmental conditions that affect food availability and hunger level in kleptoparasites (Altwegg 2003, Iyengar 2008) may influence the rate and success of kleptoparasitism (Brockmann and Barnard 1979). Previous studies have shown that kleptoparasitism is more common when weather (including the effect of wind on sea roughness and visibility), and/or other physical conditions preclude the kleptoparasite from feeding on its own (e.g., food shortage, Dunn 1975, Grubb 1978, Favero et al. 1997, Katchikian et al. 2002, García and Mariano Jelicich 2005).

Many studies have reported terns as victims of kleptoparasitic behavior by gulls or other terns during the breeding season (Fuchs 1977, Quintana and Yorio 1999, Dies and Dies 2005). In contrast to many seabirds, most terns do not swallow prey after capturing it but hold it in their bill during transport, visible to other birds and increasing the likelihood of kleptoparasitic attack. At Punta León, Patagonia, Argentina, the Royal (*Thalasseus maximus*) and Cayenne Terns (*T. sandvicensis eurygnatha*) breed sympatrically with the Kelp Gull (*Larus dominicanus*) (Yorio and Efe 2008). In Patagonia, the Kelp Gull is a generalist forager, feeding not only on intertidal invertebrates and fish but also taking advantage of artificial food sources such as garbage dumps and refuse from fisheries (Bertelotti and Yorio 1999, 2000). Kelp Gulls feed frequently on the coast of Punta León, characterized by an extensive rocky intertidal zone where food availability strongly depends on the tide and other environmental conditions. Although previous studies have described the opportunistic kleptoparasitic interaction between gulls and terns (e.g., Fuchs 1977, Quintana and Yorio 1999, Dies and Dies 2005, Seco Pon and Morettini 2009), several aspects of it remain unexplored, particularly the ecological and environmental conditions affecting the rate of this behavior. Only a few tests of the interplay of prey quality and environmental conditions as triggers of kleptoparasitism have been published.

With this background, our goals were (1) to describe the kleptoparasitism of gulls on terns qualitatively and quantitatively and (2) to compare the effect of prey quality and environmental conditions triggering kleptoparasitism by Kelp Gulls on Royal and Cayenne Terns. To address our second objective, we used an information-theoretic approach (Burnham and Anderson 2002) by constructing a set of a priori candidate models as hypotheses. By comparing support for the models and interpreting estimates of the parameters in them, we determined which hypothesized factors had more effects on the rate of kleptoparasitism. We predicted that environmental conditions primarily would explain the rate of kleptoparasitism, given their effects on food availability for potential kleptoparasites.

METHODS

STUDY AREA

We undertook this study during the breeding season of 2006 at Punta León Provincial Reserve (43° 04′ S, 64° 29′ W, Patagonia, Argentina). The coast in this area is characterized by extensive coastal cliffs 30–100 m high, gravel beaches, and an extensive rocky intertidal zone (vertical range of the tide up to 6 m during spring tides). A silt platform of approximately 5 ha lying to the seaward side of the cliffs is covered by vegetation consisting mainly of *Suaeda divaricata*, *Atriplex lampa*, and *Lycium chilense* and is used as a nesting site by several species of seabirds, including the Kelp Gull (5600 pairs), Royal Tern (450 pairs), Cayenne Tern (1050 pairs), Imperial Cormorant (*Phalacrocorax atriceps*; 3000 pairs), and Neotropic Cormorant (*P. brasiliensis*; 100 pairs) (Yorio et al. 1994, Gatto and Yorio 2009). At this multi-species colony, gulls interact with terns during incubation and chick rearing through predation, kleptoparasitism, and competition for nest sites (Quintana and Yorio 1998, 1999). During our study, we noted no interactions between cormorants and terns, and no such interactions have been mentioned in the literature.

In the study area, Royal and Cayenne Terns lay eggs during the second week of October, chicks hatch during the second or third week of November, and chicks fledge at approximately 3 weeks of age to form mixed crèches along the beach. Nests of both species of terns are mingled and placed in the center of the multi-species colony, surrounded by Kelp Gull and cormorant nests. The density of tern nests ranges from 9 to 11 nests per m^2 (Yorio et al. 1994, Quintana and Yorio 1998).

BEHAVIORAL OBSERVATION AND DATA GATHERING

To obtain information about kleptoparasitism of Kelp Gulls on Royal and Cayenne Terns, we made observations (throughout daylight hours, 08:00–20:00 local time) from a mobile blind that allowed an approach of up to 3 m from the nesting terns without signs of disturbance. During each hour of observation ($n = 65$ hr distributed over 20 days) we followed with the help of binoculars (8× magnification) terns entering the colony with prey in their bills (a total of 1957 terns with prey observed). Terns were not banded; we kept repeated sampling of

TABLE 1.   Total fresh weight and energy content estimated for categories of prey of Royal and Cayenne Terns at Punta León Provincial Reserve, Chubut, Argentina.

	Size[a]	Silversides (*Odontesthes* spp.[b])	Argentine anchovy (*Engraulis anchoita*)	Butterfish (*Stromateus brasiliensis*)
Total fresh weight (g)				
	S	0.4	2.7	1.5
	M	1.0	4.3	3.1
	L	2.1	6.7	6.2
	VL	4.7	10.7	12.5
Energy content (kJ g wet weight^{-1})		5.2	6.2	5.4
Energy content (kJ prey^{-1})	S	2.1	16.7	8.1
	M	5.2	26.6	16.7
	L	10.9	41.5	33.5
	VL	24.5	66.3	67.5

[a]Small (S), less than 0.5× length of bill; medium (M), 0.5–1× length of bill; large (L), 1–1.5× length of bill; very large (VL), >1.5× length of bill.
[b]*Odontesthes incisa*, *O. smitti*, and *O. argentinensis* pooled.

individuals to a minimum by selecting different patches in the colony during each observation period. Observations lasted until the prey was eaten by the adult, delivered to the chick, or stolen by a kleptoparasite. We considered an attack successful when the kleptoparasite took the fish either from the chick or the adult tern. For each attack we recorded the size and type of prey (see below for details), the chick's age, delivery time (i.e., time elapsed from the moment at which a tern arrives at the nest with the fish in its bill until the moment the prey is taken by its chick), handling time (i.e., time elapsed from the moment the fish is taken by the chick to the time the prey is swallowed), and environmental variables (wind direction, wind intensity, and tidal level).

We categorized chicks as (1) younger than 1 week of age (chicks that remain at the nest, or do not move more than 0.5 m from their nest), (2) between 1 and 3 weeks of age (chicks that leave the nests for short periods but return to the nest regularly), and (3) older than 3 weeks (chicks already in crèches around the periphery of the colony) (see Quintana and Yorio 1999).

We made our observations under various weather conditions (recorded by a permanent weather station through the whole breeding season) and stages of the tidal cycle (noted by the observer). We recorded wind intensity as a continuous variable. During the study wind speeds averaged 4 m sec^{-1}; gusts reached 28 m sec^{-1}). Because the shoreline runs from northeast to southwest (roughly 45° to 225°), we categorized wind direction as (1) between 46° and 135°, (2) between 136° and 225°, (3) between 226° and 315°, or (4) between 316° and 45° (this last direction was never recorded, so we considered only the first three categories). We categorized the tide as low (when ≥ 25% of the intertidal area was exposed) or high (<25% of the intertidal was exposed).

TYPE, SIZE, AND QUALITY OF PREY

We identified fish prey to the lowest taxonomic level possible by their morphology in comparison with prey accidentally left by adults among the nests. To reduce biases in the determination and characterization of prey, the same observer made all observations of feeding. Three prey types were identified: Argentine anchovy (*Engraulis anchoita*), silversides (*Odontesthes incisa*, *O. smitti*, and *O. argentinensis* pooled together) and butterfish (*Stromateus brasiliensis*). Of the total prey items, 2% were not identified. We categorized the size of prey in relation to the adult's bill length (60.0 ± 4.3 mm, $n = 57$, for the Cayenne Tern; 65.0 ± 2.9 mm, $n = 12$, for the Royal Tern; Gatto and Yorio 2009) as small (length <0.5× that of the bill), medium (length 0.5–1× that of the bill), large (length 1–1.5× that of the bill), or very large (length >1.5× that of the bill). Given the similarity in the two terns' bill length, we assumed the length of an average bill to be 62.5 mm.

To determine prey quality (in kJ g^{-1} wet weight), we collected the main fish prey (Argentine anchovy, silversides, and butterfish) from artisanal fisheries operating in areas where the terns forage. Samples were placed in bags to prevent dehydration and frozen. In the laboratory, we weighed each specimen (to 0.001 g) and measured its maximum length (to 0.1 mm). We developed empirical linear regressions and estimated prey mass (M, in grams fresh weight) from total length (L, in mm) by these functions: Argentine anchovy, $M = 2.16e^{0.015L}$ ($R^2 = 0.80$, $n = 20$); silversides, $M = 0.28e^{0.026L}$ ($R^2 = 0.96$, $n = 36$); butterfish, $M = 1.06e^{0.0234L}$ ($R^2 = 0.90$, $n = 20$). Then we estimated the median mass of a fish of each size class as described above (see Table 1).

To estimate energetic content of prey, we chopped, homogenized, and dried the soft tissues in an oven at 60–80 °C

for 24–72 hr to a constant weight. For each type of prey, to determine wet and dry weights (to the nearest 0.001 g), we weighed the homogenate before and after drying. The energy content of each type of prey was estimated with the empirical linear model for marine Patagonian fish, which uses the percentage of dry weight to calculate energy density (energy density $= -2.868 + 326 \times$ dry weight, $R^2 = 0.94$; see Ciancio et al. 2007 and Table 1).

STATISTICAL ANALYSES

We compared the rate and efficiency of kleptoparasitism of the Kelp Gull on the Royal and Cayenne Terns with separate χ^2 tests (Zar 1999).

To compare the effect of prey quality and environmental conditions triggering kleptoparasitism, we used generalized linear models with a binomial error structure (two possible values for the response variable: 0 if no kleptoparasitism occurred, 1 if it did occur) and log-link function (logistic regression) (Crawley 2007). We fitted models with R software (R Development Core Team 2007).

We used an information-theoretic approach to evaluate support for alternative a priori models, to estimate parameter values, and to test our hypotheses concerning the effects of prey quality and environmental factors on the rate of kleptoparasitism (Burnham and Anderson 2002, Crawley 2007). Our set of twelve a priori candidate models included prey-quality-effect models with prey type and prey size; environmental-effect models with wind intensity, wind direction, and tidal height; models consisting of all two-way combinations within prey quality and within environmental factors; a global model with all effects; and a null model with just an intercept. Small prey was not considered in the models, as kleptoparasitism did not occur when these prey items were delivered (see Nicholls 1989).

Model selection was based on Akaike's information criterion corrected for lack of independence and small sample sizes (QAIC$_c$; Burnham and Anderson 2002). We assessed the fit of models by visually inspecting plots of standardized deviance residuals for global models. We estimated the quasi-likelihood adjustment for overdispersion ($\hat{c}$) from global models (Burnham and Anderson 2002). We used two measures to provide further insight into the amount of uncertainty in model selection. The first was the difference in QAIC$_c$ between the best approximating model and all the other models (Burnham and Anderson 2002), termed ΔQAIC$_c$. In general, a ΔQAIC$_c$ score between 0 and 2 indicates substantial support for the model, a ΔQAIC$_c$ between 4 and 7 indicates much less support for the model, and a ΔQAIC$_c > 10$ indicates essentially no support for the model (Burnham and Anderson 2002). The second measure calibrates models to provide relative plausibility by normalizing each model on the basis of its ΔQAIC$_c$ value, termed "model weight" (Anderson and Burnham 1999, Burnham and Anderson 2002). Parameter estimates were calculated by the technique of model averaging (model-averaged inference) from QAIC$_c$ weights for all candidate models (Burnham and Anderson 1998). Unconditional variances of those candidate models were used to calculate standard errors. To supplement evidence of important effects with parameter likelihoods, we also assessed the degree to which the 95% confidence intervals of parameter estimates overlapped zero. We calculated upper and lower confidence limits by adding or subtracting $2 \times$ SE, respectively.

RESULTS

GENERAL CHARACERISTICS OF THE TERN–GULL SYSTEM

In general terms, the gulls' kleptoparasitic behavior can be described as follows: kleptoparasitic gulls remained at the periphery of the tern colony (either on the ground or perched in a bush) or flew over the tern colony looking for opportunities for kleptoparasitism. Kleptoparasitic attacks happened while food was being transferred from the adult tern's bill to the chick, or it was taken directly from chicks that did not swallow the fish immediately after the parent delivered it. During this study, we did not observe Kelp Gulls kleptoparasitizing food from terns while in flight.

The rate of kleptoparasitism (percentage of attempted kleptoparasitic attacks out of total prey deliveries observed) was higher for the Royal than for the Cayenne Tern (Royal: 17.7%, $n = 1152$ observed feedings; Cayenne: 5.6%, $n = 805$ feedings; $\chi^2_1 = 49.1$, $P < 0.001$). However, the efficiency of kleptoparasitism (percentage of successful attacks out of total kleptoparasitic attacks registered) on the Royal (41.9%) and on the Cayenne (42.2%; $\chi^2_1 = 0.001$, $P > 0.97$) did not differ. Thus, Kelp Gulls robbed significantly more food from Royal Terns; whereas 7.4% ($n = 1152$) of food brought by Royal Terns was successfully stolen, only 2.4% ($n = 805$) was taken from Cayenne Terns ($\chi^2_1 = 21.5$, $P < 0.001$).

The most common prey of the Royal Tern was the Argentine anchovy (62.4%; $\chi^2_2 = 535.86$, $P < 0.001$), whereas silversides constituted the bulk of prey of the Cayenne Tern (62.1%; $\chi^2_2 = 350.55$, $P < 0.001$; Fig. 1). Royal Terns tended to feed chicks younger than one week old with silversides and Argentine anchovies. As the chicks grew, silversides were replaced by Argentine anchovies and butterfish. For the Cayenne Tern, the pattern was similar, but silversides constituted an important prey delivered to all ages of chicks (Fig. 2). The size of prey delivered by adults increased with the chicks' age (silversides: Spearman rank correlation, $r_s = 0.37$, $n = 707$, $P < 0.001$; Argentine anchovies: Spearman rank correlation, $r_s = 0.45$, $n = 676$, $P < 0.001$; butterfish: Spearman rank correlation, $r_s = 0.29$, $n = 110$, $P < 0.02$). Delivery times decreased with the chick's age (Spearman rank correlation, $r_s = -0.62$, $n = 1790$, $P < 0.001$), and for chicks of all ages handling time was remarkably short, less than 1.16 ± 4.33 sec ($n = 1957$).
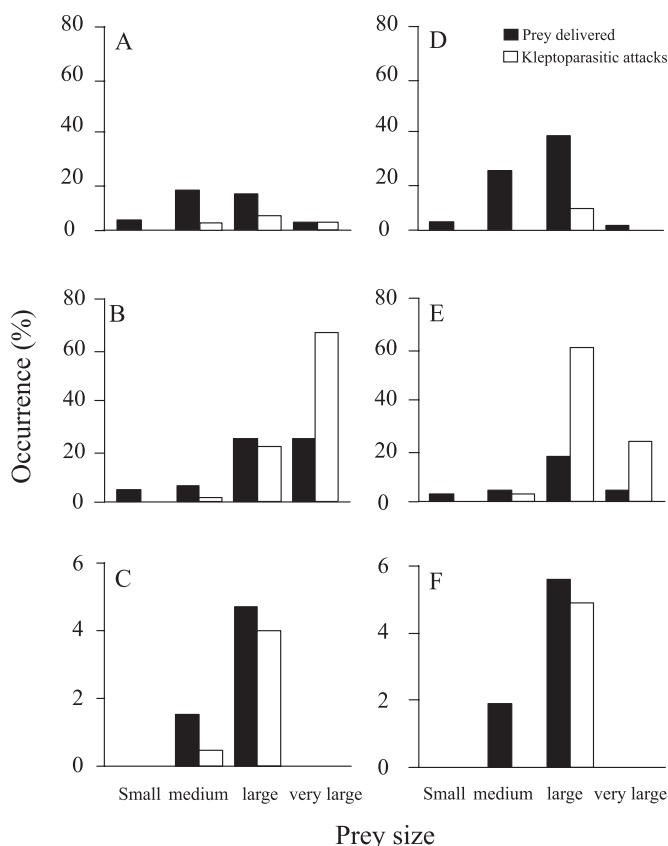
FIGURE 1.   Relative importance of prey brought to the colony and kleptoparasitic attacks in Royal (A, B, C) and Cayenne (D, E, F) Terns. Silversides are shown in the top, anchovies in the middle and butterfish in the lower panels. Number of prey brought and kleptoparasitic attacks were 1129 and 200 for Royal, and 781 and 41 for Cayenne Terns, respectively. Note different y-axis scale in C and F versus in the other graphs.

FIGURE 2.   Distribution of occurrences for the major prey items brought to Royal (A) and Cayenne (B) Terns' chicks of different age.

The percentage of prey kleptoparasitized from Royal Tern chicks increased with the chicks' age (11.4, 16.8, and 22.2% at the first, second, and third stage, respectively; $n = 736$, $\chi^2_2 = 12.9$, $P < 0.001$). The rate of kleptoparasitism on the Cayenne Tern was at its maximum during the second stage (1.9, 9.2, and 4.7 % at the first, second, and third stage, respectively; $n = 1035$, $\chi^2_2 = 16.4$, $P < 0.001$).

FACTORS AFFECTING THE RATE OF KLEPTOPARASITISM

We found support for our hypothesis concerning the effects of prey quality (i.e., prey type and size) on the rate of kleptoparasitism by Kelp Gulls on Royal Terns. However, we also found support for our global model with all effects; the global model explaining rate of kleptoparasitism fit our data well (variance-inflation factor, $\hat{c} = 0.78$). Both prey type and prey size were important in explaining the rate of kleptoparasitism. This model did not account for more than 23% of the variation
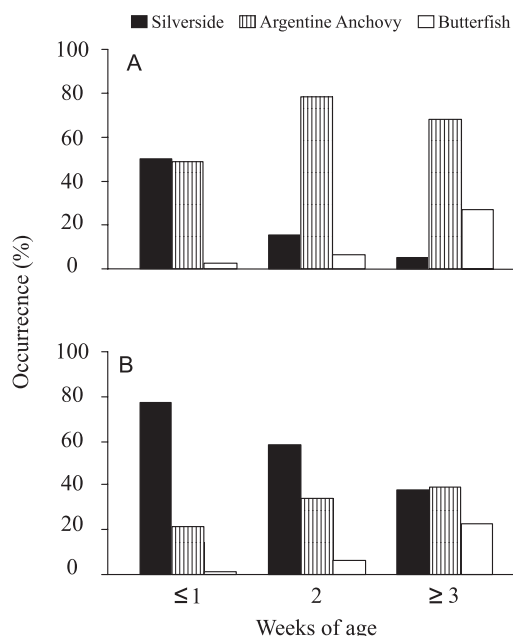
in rate of such behavior (Table 2). The rate of kleptoparasitism increased with prey size; the parameter estimate was between 1.5 and 3.5 times higher when Royal Terns captured large and very large prey than when they captured medium prey. With respect to prey type, the parameter estimate was

TABLE 2.   A priori candidate models explaining the rate of kleptoparasitism by Kelp Gulls on Royal Terns (956 delivery cases included in the models). Number of parameters (K) in each model included the intercept and each explanatory variable. Models with a lower $\Delta QAIC_c$ and a greater $\Delta QAIC_c$ weight have more support.

Model	K	$\Delta QAIC_c$	$\Delta QAIC_c$ weight	R^2
Prey size + prey type	5	0.0	0.59	0.23
Global	9	0.7	0.41	0.24
Prey type	3	14.3	0.00	0.22
Prey size	3	165.3	0.00	0.01
Wind direction + wind intensity	4	273.1	0.00	0.01
Wind intensity + tidal height	3	273.2	0.00	<0.01
Wind direction + wind intensity + tidal height	5	274.1	0.00	0.01
Wind intensity	2	271.8	0.00	<0.01
Wind direction + tidal height	4	280.1	0.00	<0.01
Tidal height	2	281.1	0.00	<0.01
Wind direction	3	279.7	0.00	<0.01
Null	1	279.8	0.00	—

TABLE 3.   Parameter estimates (± SE) from generalized linear models describing the rate of kleptoparasitism by Kelp Gulls on Royal Terns. Parameter likelihoods are QAIC$_c$ weights summed across all models that contained that parameter and are indicative of the importance of the variable. Parameter estimates are weighted averages (using QAIC$_c$ weights) from all models, and standard errors (SE) are calculated for all candidate models from unconditional variances. Upper and lower confidence limit intervals (95%) were calculated adding or subtracting 2 SE, respectively.

Explanatory variable	Category	Parameter likelihood	Parameter estimate ± SE	Confidence interval Lower	Upper
Intercept			−4.71 ± 0.56	−5.84	−3.57
Prey size		1.00			
	Large		1.63 ± 0.43	0.78	2.48
	Very large		3.40 ± 0.43	2.53	4.26
Prey type		0.99			
	Argentine anchovy		1.10 ± 0.29	0.51	1.70
	Butterfish		1.26 ± 0.43	0.40	2.12
Wind direction		0.41			
	136°–225°		0.55 ± 0.28	−0.01	1.10
	226°–315°		0.03 ± 0.22	−0.40	0.47
Wind intensity		0.41	0.16 ± 0.07	0.03	0.30
Tidal height	Low	0.41	0.01 ± 0.19	−0.42	0.44

approximately 1.2 times higher when Royal Terns captured butterfish and Argentine anchovies than when they captured silversides (Fig. 1, Table 3). In our set of a priori candidate models for environmental effects we did not find evidence that environmental factors (i.e., tidal stage, wind direction and intensity) affected the rate of kleptoparasitism.

TABLE 4.   A priori candidate models explaining the rate of kleptoparasitism by Kelp Gulls on Cayenne Terns (694 delivery cases included in the models). Number of parameters (K) in each model included the intercept and each explanatory variable. Models with a lower ΔQAIC$_c$ and a greater ΔQAIC$_c$ weight have more support.

Model	K	ΔQAIC$_c$	ΔQAIC$_c$ weight	R^2
Prey size + prey type	5	0.0	0.82	0.27
Global	9	3.1	0.18	0.28
Prey size	3	63.0	0.00	0.23
Prey type	3	142.0	0.00	0.11
Wind direction + wind intensity + tidal height	5	251.4	0.00	0.03
Wind direction + wind intensity	4	253.5	0.00	0.02
Wind intensity + tidal height	3	256.7	0.00	0.01
Wind intensity	2	259.8	0.00	<0.01
Null	1	266.2	0.00	—
Tidal height	2	262.7	0.00	<0.01
Wind direction + tidal height	4	265.9	0.00	<0.01
Wind direction	3	268.9	0.00	<0.01

For the Cayenne Tern, as for the Royal Tern, we found the most support for our hypothesis concerning effects of prey quality on the rate of kleptoparasitism, but there was also some support for our global model with all effects (Table 4). The global model explaining rate of kleptoparasitism fit our data, but the variance-inflation factor ($\hat{c} = 0.33$) indicated slight underdispersion. Again, prey type and prey size were important in explaining the rate of kleptoparasitism. This model accounted for 27% of the variation in rate of such behavior (Table 4). Kleptoparasitism rates increased as prey size increased; the parameter estimate was 2.5 times higher when Cayenne Terns captured large and very large prey (Table 5). For prey type, the parameter estimate was between 3.2 and 1.5 times higher when Cayenne Terns captured Argentine anchovies and butterfish then when they captured silversides (Fig. 1, Table 5). As for the Royal Tern, we did not find evidence in our set of a priori environmental-effect models that environmental factors affected the rate of kleptoparasitism.

DISCUSSION

Kelp Gulls kleptoparasitized the Royal more than the Cayenne Tern. Although the rate of kleptoparasitism of both species was relatively low (see Furness 1987), the efficiency of kleptoparasitism was high. Gulls kleptoparasitized approximately 8% of the food brought back to the colony by adults Royal Terns. These results are in line with those of a previous study at the same colony in early 1990s (Quintana and Yorio 1999), although those results were based on a small sample. Quintana and Yorio (1999) proposed that the higher rate of kleptoparasitism on Royal Terns could be explained by an apparent difference in

TABLE 5.   Parameter estimates (± SE) from generalized linear models describing the rate of kleptoparasitism by Kelp Gulls on Cayenne Terns. Parameter likelihoods are QAIC$_c$ weights summed across all models that contained that parameter and are indicative of the importance of the variable. Parameter estimates are weighted averages (using QAIC$_c$ weights) from all models, and standard errors (SE) are calculated from all candidate models from unconditional variances. Upper and lower confidence limit intervals (95%) were calculated adding or subtracting 2 SE, respectively.

Explanatory variable	Category	Parameter likelihood	Parameter estimate ± SE	Confidence interval Lower	Confidence interval Upper
Intercept			−6.88 ± 0.66	−8.20	−5.56
Prey size		1.00			
	Large		2.24 ± 0.59	1.07	3.42
	Very large		2.88 ± 0.62	1.63	4.13
Prey type		1.00			
	Argentine anchovy		3.15 ± 0.35	2.45	3.85
	Butterfish		1.52 ± 0.53	0.46	2.57
Direction wind		0.17			
	136°–225°		0.42 ± 0.32	−0.21	1.05
	226°–315°		−0.76 ± 0.39	−1.54	0.02
Wind intensity		0.17	0.14 ± 0.08	−0.89	−0.02
Tidal height	Low	0.17	−0.33 ± 0.28	−0.89	0.22

the two species' diet. Those authors, however, were unable to confirm the type and size of prey adults delivered to chicks. In our study we found that Royal Terns brought back to the colony prey of higher quality than did Cayenne Terns. This fact could make the Royal Tern a more profitable target for the Kelp Gull to kleptoparasitize.

We found anchovies and silversides, respectively, to be among the major food items in the diet of the Royal and Cayenne Terns. Additionally, Royal Terns delivered bigger fish than did Cayenne Terns, results in agreement with those published by Gatto and Yorio (2009) for the same colony. These results may indicate that prey size and type could be acting as mechanisms of resource partitioning between the two tern species (Gatto and Yorio 2009). Such a mechanism has been reported in several studies of seabirds (e.g., Ashmole and Ashmole 1967, Fasola et al. 1989, Ballance et al. 1997, Croxall et al. 1997).

Several studies have examined how parents regulate (in terms of prey size and type) food delivery during their chicks' development. For example, some species that feed their chicks regularly seem to be able to adjust provisioning in accordance with the chick's energy requirements (Asmussen 2006, Stienen 2006). At Punta León, prey brought to the chicks varied through the season, and food delivered by both tern species seemed to be adjusted to in proportion to the chicks' size-related mechanical restrictions and energetic requirements. Smaller fish were important early in the season, but, as the season progressed, larger prey with higher energy content became more common. Delivery times shortened as the season progressed, likely due to the chicks' increasing skills in taking prey delivered by their parents. However, it is noteworthy that in spite of relatively longer delivery times observed in chicks

younger than one week of age, the incidence of kleptoparasitism at this age was lower than that at later ages. The fact that for the Royal Tern the rate of kleptoparasitism increased with the chicks' age in but for the Cayenne Tern the rate was higher when chicks were of age category 2 could be at least partially attributed to the Royal Tern's bringing high-quality prey (i.e., large and very large anchovies and butterfish) to the colony later in the season.

FACTORS AFFECTING KLEPTOPARASITISM

Previous studies have shown that kleptoparasitism by gulls is influenced mainly by prey quality and environmental conditions (e.g., Hulsman 1984, Khatchikian et al. 2002, Morand-Ferron et al. 2006, Stienen 2006). However, none of these studies compared the effect of these variables as we did.

Environmental factors affect various aspects of birds' foraging behavior, including hunting success, energy intake, foraging strategy, microhabitat selection, and likelihood of kleptoparasitism (e.g., Schnell 1968, Grubb 1977, Dugan 1982, Temeles and Wellicome 1992, Katchikian et al. 2002, García and Mariano Jelicich 2005). For example, wind intensity and direction may affect sea-surface roughness and water turbidity and consequently availability of food for birds (Taylor 1983, Stienen et al. 2000). Seabirds are highly susceptible to changes in food availability, in particular during the breeding season, when they are confined to feeding areas relatively close to the colony (Stienen 2006). These changes in food availability may trigger facultative switches to kleptoparasitism. In our study, however, the evidence did not support our prediction about the effect of environmental conditions triggering kleptoparasitism. On the contrary, we found that

prey quality (prey type and size) promoted kleptoparasitism. Several studies have shown that terns carrying large prey are more likely to be victims of kleptoparasitism because of the increased handling time larger prey require (Brockmann and Barnard 1979, Steele and Hockey 1995). In our study, however, we found handling times for prey of all sizes and types to be very short. More valuable prey (i.e., "large" and "very large" anchovies and butterfish) were more likely to trigger kleptoparasitism (see Table 1) in spite of the very short handling times observed.

Two conflicting selection pressures could determine the size of fish selected by the terns: (1) the need to provide chicks with adequate quality and quantity of food and (2) the need to minimize the loss of fish to kleptoparasitism. To reduce the amount of time and energy spent flying to and from the colony looking for and carrying food, terns should make the smallest number of fishing trips possible. To achieve this, a tern should take prey that not only provides the highest net energy to the young but also minimizes the risk of kleptoparasitism. In our study, we found that the size and type of prey delivered by adult terns changed through the season, with energy content per prey and risk of kleptoparasitism increasing. However, the lack of data on prey selectivity and the length of foraging trips, among other variables, precludes further analysis of foraging efficiency and decisions made by terns to cope with the costs of kleptoparasitism.

Our study shows (1) the importance of prey quality triggering gulls' kleptoparasitism of terns and (2) that kleptoparasitic gulls can remove an important (~12% in biomass) portion of food brought to a Royal Tern colony. Further studies are needed to assess the effect of kleptoparasitism by Kelp Gulls on tern chicks' growth rate and survival.

ACKNOWLEDGMENTS

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