Interspecific kleptoparasitism by Brown-headed Gulls (*Chroicocephalus maculipennis*) on two hosts with different foraging strategies: a comparative approach

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Abstract. Kleptoparasitism is a well known foraging strategy used opportunistically by many seabirds. Our study compares the strategies performed by a facultative kleptoparasite species, the Brown-hooded Gull (*Chroicocephalus maculipennis*), associated with two hosts with different foraging strategies, the American Oystercatcher (*Haematopus palliatus*) and Red-gartered Coot (*Fulica armillata*). In total, 97% of the prey items stolen from Oystercatchers were the clam *Tagelus plebeius*, and all prey items stolen from Coots were the crab *Cyrtograpsus angulatus*. The attack rate by Gulls (number of kleptoparasitic attacks per unit time) did not differ significantly between Oystercatchers and Coots, but the success rate of attacks (successful kleptoparasitic attacks as a proportion of total attacks) was greater for attacks on Coots than on Oystercatchers. The mean rate of feeding (number of stolen items ingested per minute) by Brown-hooded Gulls did not differ with host. Gulls strongly selected large prey when stealing food. The comparison of net intake (cost–benefit balance) for each kleptoparasite–host system showed that profitability was 3.5 times higher when kelptoparsitising Coots than when stealing from Oystercatchers. We suggest future work should study in more detail the costs and benefits for kleptoparasites with multiple hosts in similar systems elsewhere.

Additional keywords: facultative kleptoparasite, foraging strategy.

Introduction

Animals engage daily in a variety of activities among which obtaining food is of paramount importance. The foraging behaviour of any individual can be analysed in terms of costs and benefits (MacArthur and Pianka 1966) and, according to optimal foraging theory, organisms should maximise net energy gain per unit of foraging time (Krebs and Davies 1993). Social foragers can either avoid or minimise costs in the foraging cycle by parasitically exploiting food that another forager has already made available (i.e. social parasitism; Giraldeau and Caraco 2000). Parasitic interactions over food are one of the most widespread forms of exploitation both within and among species (Barnard 1984) and there is a vast literature describing the many forms that such parasitic foraging can take, such as local enhancement (Thorpe 1956), area copying (Krebs *et al*. 1972), social facilitation (Curio 1976), joining (Giraldeau and Lefebvre 1986) and kleptoparasitism (Rothschild and Clay 1952).

Kleptoparasitism is a form of competition that involves stealing food already procured by another forager, and is one of the most common types of exploitation between animals (Giraldeau and Caraco 2000). Recent examples of this behaviour have been reported in snails (Iyengar 2004), insects (Benttinen and Preisser 2009), spiders (Kerr 2005), fish (Hamilton and Dill 2003), lizards (Cooper and Pérez-Mellado 2003), birds (García *et al*. 2010; Varpe 2010) and carnivorous mammals (Carbone *et al*. 2005). Observations of birds as kleptoparasites are among the most detailed studies. The extensive review by Brockmann and Barnard (1979) provides a list of observations and notes of kleptoparasitism by birds and shows that the behaviour is much more common in some groups than in others, and especially common in seabirds (Furness 1987). Some seabirds, such as skuas and jaegers (*Stercorarius* spp.), can be specialised kleptoparasites. Others, such as gulls and terns (Laridae), may kleptoparasitise opportunistically (i.e. facultative kleptoparasites) 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).

The Brown-hooded Gull (*Chroicocephalus maculipennis*) is endemic to southern South America (Burger and Gochfeld 1996); it has a wide distribution in Argentina that includes coastal and inland areas (Escalante 1970). Previous studies indicate this species has a generalist diet, including live prey (e.g. insects, crustaceans, molluscs and fish), carrion, refuse and prey obtained by kleptoparasitism (Escalante 1970; Khatchikian *et al.* 2002; Ghys and Favero 2004). Kleptoparasitism by Brown-hooded Gulls on the American Oystercatcher (*Haematopus palliatus*) and the Red-gartered Coot (*Fulica armillata*) has been reported in the Mar Chiquita coastal lagoon of Buenos Aires Province, Argentina (Martínez and Bachmann 1997; Khatchikian *et al.* 2002; García *et al.* 2008). Brown-hooded Gulls steal from both hosts when all three species are present during the non-breeding season. At this site, the American Oystercatcher feeds mainly on the Stout Razor Clam (*Tagelus plebeius*) and the Red-gartered Coot feeds on the mud crab *Cyrtograpsus angulatus*, two major components of the benthic fauna in south-western Atlantic estuaries (Gutiérrez *et al.* 2000; Spivak *et al.* 1994). Through kleptoparasitism, Gulls can acquire prey that they would be unable to access directly owing to morphological or behavioural restrictions (see Brockmann and Barnard 1979; Duffy 1980; Furness 1987). Although the mud crabs could be accessible in shallow waters during spring–summer, in winter they are distributed in deeper waters (Gavio 2004), and thus not available for Gulls through plunge-diving in the foraging patches frequented by Coots where kleptoparasitism was observed. Moreover, there is no literature in the study area reporting Brown-hooded Gulls feeding on Clams, besides those kleptoparasitised from Oystercatchers; Gulls seem otherwise to be unable to locate clams in the substrate or to separate the valves to access the soft tissues.

Given this background, our main objective was to analyse and compare the kleptoparasitic strategies of Brown-hooded Gulls associated with two hosts with different foraging strategies. We hypothesised that the strategies of the opportunistically kleptoparasitic Brown-hooded Gulls are affected by the feeding behaviour of the host species. We examine this through variation in the foraging tactics used to capture prey, the type of prey in dispute, and the handling methods and duration of handling of the different prey.

Materials and methods

Study area

This study was conducted at Mar Chiquita coastal lagoon, Buenos Aires Province, Argentina (37°46′S, 57°27′W), which is a provincial reserve and also a UNESCO Man and the Biosphere Reserve (Iribarne 2001). The coastal lagoon is $46 \, km^2$ of tidal brackish water and mudflats, surrounded by a large area of marshes dominated by the halophyte *Spartina densiflora* (Spivak *et al.* 1994; Iribarne *et al.* 1997). Intertidal benthic communities here, and in other south-western Atlantic estuaries, are characterised by very low macroinfaunal diversity. The Stout Razor Clam (*Tagelus plebeius*), and the polychaetes *Laeonereis acuta*, *Heteromastus similis*, *Neanthes succinea* and *Nephtys fluviatilis* are the numerically dominant species (Botto *et al.* 1998; Gutiérrez *et al.* 2000). The dominant epibenthic organisms are the varunid crabs *Neohelice granulata* and *Cyrtograpsus angulatus* (Boschi 1964; Spivak *et al.* 1994).

Behavioural observations

We quantified the kleptoparasitic behaviour of Brown-hooded Gulls by focal sampling (Martin and Bateson 1993) of individual Gulls associatign with either American Oystercatchers or Red-gartered Coots. Observations were made between April and September from 2004 to 2007. We recorded 107 focal observations in which kleptoparasitism by Brown-hooded Gulls occurred (67 on Oystercatchers and 40 on Coots), with an average duration of the focal observation of $9.6 \pm 3.8 \, min$ (s.d.). In order to compare the prey stolen by Gulls (125 items taken from Oystercatchers and 83 from Coots) with prey captured by the hosts (as an indicator of prey available for kleptoparasites), we also undertook focal observations of American Oystercatchers ($n = 146$ focal observations, average duration of $10.3 \pm 4.4 \, min$; 373 Stout Razor Clams captured) and Red-gartered Coots ($n = 158$ observations, average duration of $8.0 \pm 4.0 \, min$; 674 crabs captured) (for details see García *et al.* 2008, 2011). All observations were made with the help of Audubon Equinox HP binoculars ($8\times$, New York), a Nikon Spotting Scope 80/80 A telescope ($12–60\times$, New York) and an AIWA Voice Sensor Recording TP-M131 tape recorder (New York). To reduce sampling bias, all focal observations were made by the same observer using the same standardised methodology (see below). Because birds were not banded, we tried to keep repeated sampling of individuals to a minimum by selecting, during a given day, birds feeding in different foraging patches.

Time-activity budget and behavioural parameters

During each focal observation of the Gulls, the following behaviours were recorded: flying (including displacement, carrying of food and aerial chasing), swimming (including displacement and carrying of food), walking (including displacement and carrying of food), resting (no apparent activity, standing), comfort behaviour (including bathing and preening), agonistic behaviour (including postures, displacements, vocalisations and stretch threats), scavenging (only Gulls feeding on clam shells left behind by Oystercatchers) and handling (time spent in handling kleptoparasitised prey). Time-activity budgets for Brown-hooded Gulls associated with Oystercatchers and Coots were calculated as the average proportion of time spent in each behavioural category. During each focal observation, both the occurrence of kleptoparasitic attacks and their outcome were recorded. Kleptoparasitism was defined as a Gull making a direct, rapid movement towards a host that had just captured prey. Such an event was considered successful when the kleptoparasite stole the prey from the host. In addition, we also recorded the number of prey items stolen, and the type and size of prey (see below for characterisation of prey). The following parameters were estimated: (1) attack rate: the number of kleptoparasitic attacks per minute; (2) success rate: the number of successful kleptoparasitic attacks as a proportion of the total number of attacks and (3) ingestion rate: the number of prey stolen that were ingested per minute.

Type, size and quality of prey

We identified two types of prey stolen by Gulls: the Stout Razor Clam (*Tagelus plebeius*) and the mud crab *Cyrtograpsus angulatus*. The size of Clams (as total length (TL)) was estimated relative to the bill-length of the Oystercatchers (mean bill-length,

sexes combined, 75 mm; G. O. García, unpubl. data) in the following size-classes: 1, TL $\leq$ 15 mm; 2, 15 mm $<$ TL $\leq$ 30 mm; 3, 30 mm $<$ TL $\leq$ 45 mm; 4, 45 mm $<$ TL $\leq$ 60 mm; and 5, 60 mm TL $\leq$ 75 mm. For the mud crab *Cyrtograpsus angulatus*, which was identified by its distinctive shape and colour, size (carapace width (CW)) was estimated relative to the length of the bill of the Coots (mean bill-length, sexes combined, 35 mm; G. O. García, unpubl. data) in the following classes: 1, CW $<$ 15 mm; 2, 15 mm CW $<$ 25 mm; 3, 25 mm $\leq$ CW $<$ 35 mm; and 4, CW $\geq$ 35 mm.

The biomass for both types of prey was estimated using regression equations available in the literature and from our own database (Berón 2009; M. S. Addino, unpubl. data). The regression equations were built from collections of prey species during the study period, and in the same foraging patches used by hosts during observations. Prey biomass (dry weight (DW), g) was estimated by considering only soft (digestible) tissues, so hard components such as exoskeletons were excluded. Biomass was estimated from prey size as follows:

$$T.\ plebeius : \text{biomass} = 0.0224 \times e^{0.0828 \times TL}$$

$$C.\ angulatus : \text{biomass} = 0.01395 \times e^{0.132 \times CW}$$

For *T. plebeius*, $R^2 = 0.84$ ($n = 65$) and for *C. angulatus* $R^2 = 0.88$ ($n = 30$).

The energy content of each prey type was obtained from pre-existing data (G. O. García, unpubl. data): 24.0 kJ g^{-1} DW for *T. plebeius* and 20.6 kJ g^{-1} DW for *C. angulatus*. The energy content (in kilojoules per prey item) for each size-class was calculated using the estimated median biomass for that class (see Table 1).

Energy modelling and cost–benefit balance

The cost–benefit balance for Gulls stealing from American Oystercatchers and Red-gartered Coots was estimated by comparing the estimated energy intake and energy expenditure for

Table 1. Median estimated size (carapace width (CW) or total length (TL)), estimated individual biomass (dry weight) and estimated individual energy content (kJ individual^{-1}) for five size-classes of mud crabs (*Cyrtograpsus angulatus*) and Stout Razor Clams (*Tagelus plebeius*)
For each size-class, estimated dry weight (g) was calculated using the median size values for each prey size-class; dry weight comprises only digestible parts (i.e. muscles and viscera) and excludes the exoskeleton. Size of mud crabs (*Cyrtograpsus angulatus*) based on carapace width (CW): 1, CW $<$ 15 mm; 2, 15 mm $\leq$ CW $<$ 25 mm; 3, 25 mm $\leq$ CW $<$ 35 mm; and 4, CW $\geq$ 35 mm. Size of Stout Razor Clams (*Tagelus plebeius*) assessed as total length (TL): 1, TL $\leq$ 15 mm; 2, 15 mm $<$ TL $\leq$ 30 mm; 3, 30 mm $<$ TL $\leq$ 45 mm; 4, 45 mm $<$ TL $\leq$ 60 mm; and 5, 60 mm $<$ TL $\leq$ 75 mm

	Size-class				
	1	2	3	4	5
Cyrtograpsus angulatus					
Median carapace width (mm)	7.50	20.00	30.00	40.00	–
Dry weight (g)	0.04	0.20	0.73	2.74	–
Energy content (kJ crab^{-1})	0.82	4.10	14.96	56.17	–
Stout Razor Clam (*Tagelus plebeius*)					
Median total length (mm)	7.50	22.50	35.50	52.50	67.50
Dry weight (g)	0.04	0.09	0.24	0.63	1.64
Energy content (kJ clam^{-1})	0.90	2.35	6.07	15.77	40.96

kleptoparasitism of each host. Intake (kJ min^{-1}) was estimated by summing the energy content of individual kleptoparasitised prey per focal observation. In those cases where the size of a prey item could not be estimated ($n = 19$), the missing data were replaced by a modal prey-size within a given focal observation. Where Gulls scavenged on Clam remains left by Oystercatchers ($n = 185$), the energy intake was assumed to be 10% of the total (mean) prey biomass. The size of this prey is a mean prey size.

Energy expenditure (kJ min^{-1}) for each Gull per focal observation was estimated by combining the basal metabolic rate (BMR, kJ day^{-1}) estimators of the metabolic cost for each activity and the time-activity budget. Using the proposed allometric equation for Charadriiformes of Ellis and Gabrielsen (2001) (BMR $= 2.149 \times M^{0.804}$, where M is mass (g) ($R^2 = 0.842$)), the estimated BMR of Brown-hooded Gulls was 225.08 kJ day^{-1}. The following estimators of metabolic cost were used: flying, 11$\times$BMR (Mugaas and King 1981); swimming, 4$\times$BMR (Goldstein 1988); resting, 1.5$\times$BMR (King 1974; Burger 1981); walking, 2$\times$BMR (Mugaas and King 1981); comfort behaviour, 2$\times$BMR (Burger 1981); agonistic behaviour, 4$\times$BMR (Burger 1981); and handling, 2$\times$BMR (Wooley and Owen 1978). Net energy intake for Gulls was estimated for each focal observation as the calculated energy intake minus estimated energy expenditure.

Statistical analyses

Mann–Whitney U tests were used to investigate differences between the behavioural parameters (i.e. rates of attack, success and ingestion) for the two different hosts (Zar 1999). In order to analyse selectivity of prey-size by Gulls, the distribution of prey-sizes taken by hosts and those stolen by kleptoparasites were compared using Ivlevs's index (E) (Ivlev 1961):

$$E = (r_i - p_i)/(r_i + p_i)$$

where r_i is the proportion of each item kleptoparasitised and p_i is the proportion of each item in the host diet (i.e. prey availability for the Gulls). Calculations were made for each focal observation, and values of r_i and p_i calculated as means of all proportions. Values of Ivlev's index range from –1 (complete avoidance) to +1 (exclusive selection). We calculated the Bonferroni interval for the observed proportion of prey stolen (Neu *et al*. 1974; Byers *et al*. 1984). The difference was considered significant when prey availability (expected percentage of use) did not fall within the respective confidence interval for the observed percentage in the diet.

Time-activity budgets estimated for kleptoparasitism of each host were compared using Generalised Linear Models (GLM) with binomial error structure and link function 'logit' (Crawley 2007). The effect of host species on the cost–benefit balance was analysed using the Mann–Whitney U test (Zar 1999). All analyses were carried out using R software v2.13.1 (R Development Core Team 2011). Values are reported as means $\pm$ s.d. unless noted. The level of significance in all tests was set to $P \leq 0.05$.

Results

General characteristics of kleptoparasite-host systems

We observed 407 kleptoparasitic attacks by Brown-hooded Gulls: 273 on American Oystercatchers and 134 on Red-gartered

Coots. Although both hosts frequently occurred in single-species flocks (of up to eight Oystercatchers and 70 Coots) with up to 20 Gulls associated, all observed kleptoparasitic attacks were performed by single gulls on single hosts.

The attack rate did not differ significantly with host species (0.42 ± 0.27 attacks min^{-1} on Oystercatchers ($n = 58$); 0.41 ± 0.23 attacks min^{-1} on Coots ($n = 36$); Mann–Whitney $U = 1030$, d.f. $= 93$, $P > 0.05$). However, the success rate was lower when attacking Oystercatchers (0.45 ± 0.31, $n = 58$) than Coots (0.57 ± 0.32, $n = 36$) ($U = 770$, d.f. $= 93$, $P = 0.03$). We found no significant differences in the ingestion rates between kleptoparasitism on Oystercatchers or Coots (0.19 ± 0.17 prey min^{-1} when stealing from Oystercatchers; 0.25 ± 0.17 prey min^{-1} when stealing from Coots; $U = 830$, d.f. $= 93$, $P = 0.09$).

Type, size and selectivity of kleptoparasitised prey

All prey items stolen from Oystercatchers ($n = 125$) were identified: with 97% the Stout Razor Clam and the rest mud crabs. The size of stolen Clams was estimated in 85% of cases, and Gulls stole clams in size-classes 2, 3 and 4 (Fig. 1a). The only four crabs stolen from Oystercatchers were in size-class 4. The comparison of size-distribution of Clams taken by Oystercatchers and those stolen by Gulls showed a significant selection of prey of size-class 4 and the proportion of Clams in size-classes 2,
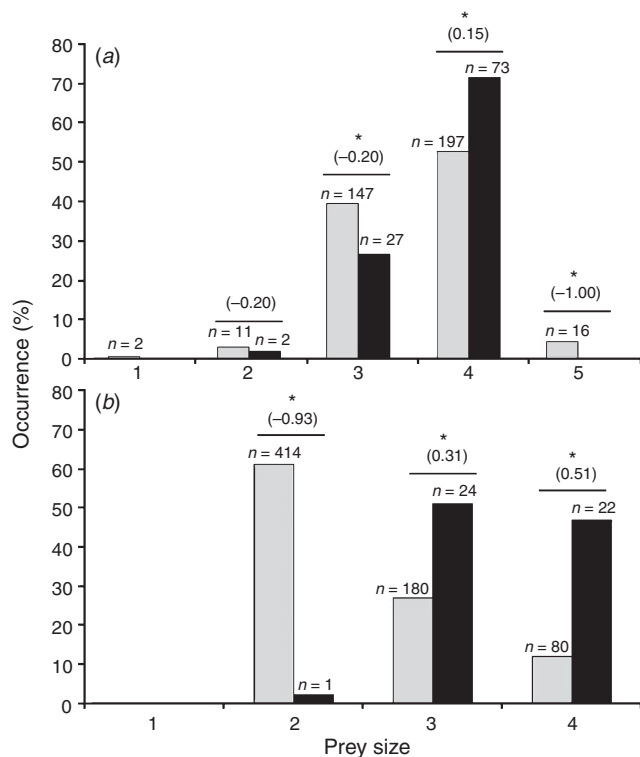
3 and 5 that were stolen was levels lower than their availablity (Fig. 1a).

All prey stolen from Coots were identified as mud crabs ($n = 83$), and size of stolen prey was estimated in all cases. Gulls stole mud crabs belonging to size-classes 2, 3 and 4. They also selected large prey, showing significant selection of crabs in size-classes 3 and 4, and avoidance for prey in size-class 2 (Fig. 1b).

Cost–benefit relationships for different hosts

The comparison of time-activity budgets for Gulls stealing from American Oystercatchers and Red-gartered Coots showed that there were significant differences between the two hosts in the following categories: swimming (GLM, $t = -14.86$, $P < 0.001$), comfort behaviour ($t = 3.20$, $P < 0.01$) and agonistic behaviour ($t = 2.07$, $P < 0.05$). The activities of flying ($t = -5.21$, $P = 0.60$) and handling ($t = 1.71$, $P = 0.08$) did not differ significantly (Fig. 2). The energy expenditure for kleptoparasitic Gulls associating with Coots (0.77 ± 0.12 kJ min^{-1}, $n = 40$) was 1.5 times higher than for Gulls associating with Oystercatchers (0.51 ± 0.17 kJ min^{-1}, $n = 63$) (Mann–Whitney $U = 240$, d.f. $= 102$, $P < 0.001$, Fig. 3a). However, the rate of energy intake was three times higher for kleptoparasitic Gulls associating with Coots (8.70 ± 7.90 kJ min^{-1}, $n = 40$) compared to those associating with Oystercatchers (2.94 ± 2.36 min^{-1}, $n = 63$) ($U = 391$, d.f. $= 102$, $P < 0.02$, Fig. 3b). The comparison of net intake by Gulls for each host showed values 3.5 times higher when stealing from Coots (7.96 ± 7.91 kJ min^{-1}, $n = 40$) compared with stealing from Oystercatchers (2.43 ± 2.36 kJ min^{-1}, $n = 63$) ($U = 397$, d.f. $= 102$, $P < 0.02$, Fig. 3c).

Discussion

As far as we know, the present study is the first comparative examination of kleptoparasitism during the non-breeding season by a species that opportunistically targets two hosts with different foraging strategies – the American Oystercatcher feeding on infaunal clams, and the Red-gartered Coot diving for crabs (Martínez and Bachmann 1997; Khatchikian *et al.* 2002; García *et al.* 2008).
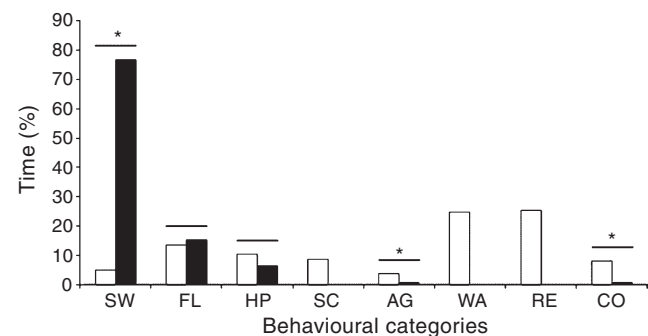
Fig. 1. Size distribution of prey-items taken by hosts (grey bars) and of items stolen by Brown-hooded Gulls (black bars): (a) Stout Razor Clams taken by American Oystercatchers; (b) mud crabs taken by Red-gartered Coots. Sample sizes are shown above bars along with Ivlev's index of prey selectivity (in parentheses). Asterisks indicate significant differences ($P < 0.05$, Bonferroni intervals).

Fig. 2. Time-activity budget of Brown-hooded Gulls associating with American Oystercatchers (white bars) and Red-gartered Coots (black bars). SW, swimming; FL, flying; HP, handling prey; SC, scavenging; AG, agonistic behaviour; WA, walking; RE, resting; and CO, comfort. Horizontal lines above bars indicate statistical comparisons performed, and asterisks denote significant differences ($P < 0.05$).
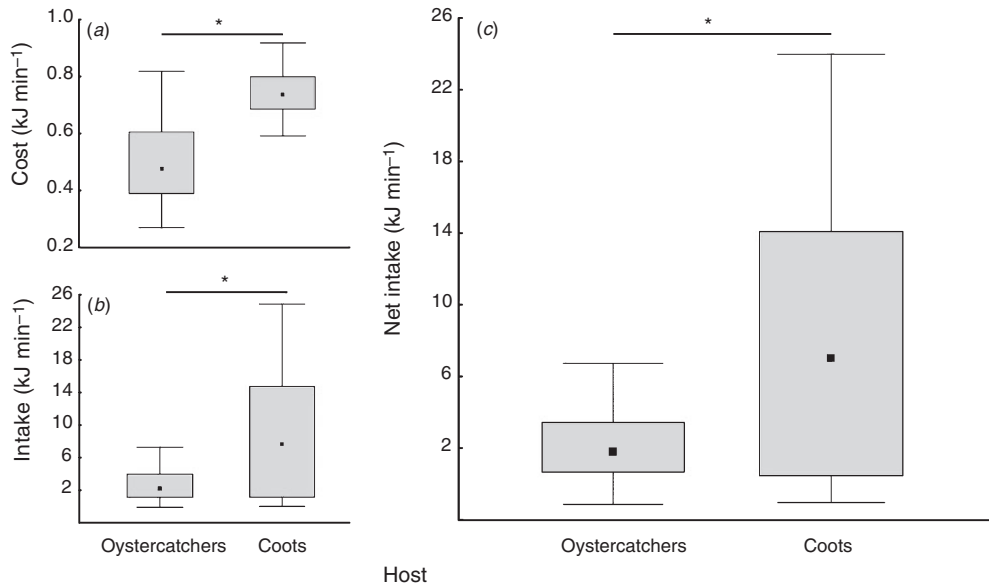
Fig. 3. (*a*) Energetic costs; (*b*) energy intake; and (*c*) net benefit of Brown-hooded Gulls kleptoparasitising either American Oystercatchers or Red-gartered Coots. Boxes are bounded by the 75th and 25th percentiles; whiskers represent minima and maxima; points inside the boxes are median values. Asterisks above horizontal lines denote significant differences between parasitism of Oystercatchers and parasitism of Coots.

Although the rate of attacks on each of the two hosts studied did not differ significantly, the success rate was higher when stealing from Coots than when stealing from Oystercatchers. In general terms, the overall estimated success rate for both hosts combined (~51%) was much greater than the median success rates presented in the review by Furness (1987) for opportunistic kleptoparasites (~23%). The high success rates observed here, for both hosts, might indicate that kleptoparasitism by Brown-hooded Gulls is practised by a small number of specialised individuals. The success rate when stealing from Coots (57%) was higher than when stealing from Oystercatchers (45%), with differences likely attributable to: (1) different tactics of defence or avoidance by hosts; (2) the aggressiveness of Gulls attacking the different host species; or (3) the efficiency with which different hosts handled the prey in presence of kleptoparasites and associated risk of injuries. Regarding defence, Coots only used escape (by swimming or diving) as an evasion tactic, whereas Oystercatchers showed a more complex repertoire of tactics including vocalisations and aggressive displays (García and Biondi 2011; García *et al*. 2011).

Brown-hooded Gulls showed strong selectivity for large kleptoparasitised prey, although Gulls never attacked Oystercatchers handling very large clams (class 5). This latter could be an artefact of the low number of samples and the low representation of this prey-size in the diet of the host or that these very large prey could, although in low proportions, be captured only by experienced Oystercatchers better at defending their prey from Gulls. Although speculative, because we lack knowledge of the life history and body conditions of observed individual Oystercatchers, the latter explanation is supported by previous studies on oystercatchers where variations in agonistic behaviour and prey captured were observed between individuals of different experience (Goss-Custard *et al*. 1982; Goss-Custard and Sutherland

1984; Goss-Custard and Le V. dit Durell 1988). The consumption of large prey by kleptoparasitic Gulls was most evident when stealing from Coots, a pattern that may be explained partly by the relationship between prey size, energy content and handling times (assuming a direct relationship between the prey size and handling time; see García *et al*. 2008, 2011). Several studies have shown that in addition to the abundance of food, the quality of available prey (in terms of size or energy content, or both) is one of the main factors triggering kleptoparasitism in seabirds (e.g. Hopkins and Wiley 1972; Brockmann and Barnard 1979; Hulsman 1984; Amat 1990; Hockey and Steele 1990; Lekuona 1999; García *et al*. 2010). The capture of larger prey also implies longer handling times, which results in the prey being visible to kleptoparasites for longer (see Brockmann and Barnard 1979; Amat 1990; García *et al*. 2008).

The main differences in the time-activity budget of Brown-hooded Gulls associating with American Oystercatchers or Red-gartered Coots could be largely attributed to differences in the foraging behaviour of the host species. When associating with Coots, Gulls spent most of their time swimming because Coots were in the water diving for crabs. When associating with Oystercatchers, Gulls appeared more passive, waiting for opportunities while Oystercatchers walked along looking for clams, although it was also evident that the Gulls spent more time in aggressive interactions with the hosts because Oystercatchers were more likely than Coots to defend themselves against kleptoparasitism. This might also be related to the narrow time-window Gulls had to perform the attack while associated with Oystercatchers, because this must be performed immediately after the clam is opened but before the Oystercatcher has eaten the prey. These fine details of the kleptoparasitic behaviour of the Gulls and the role of Oystercatchers in opening the clams for them was not studied here and may deserve further exploration.

In terms of costs, the kleptoparasitism performed by Brown-hooded Gulls demanded more energy when associating with and stealing from Coots, although these costs were readily compensated by a larger energy intake per item. It was clear then that the net benefit for Gulls kleptoparasitising Coots was higher compared to kleptoparasitism of Oystercatchers. This difference can be linked to the combination of the greater efficiency of the kleptoparasitic attacks, and the higher energy intake, when stealing from Coots. These results indicate that the kleptoparasitic association with Red-gartered Coots was more beneficial than the association with American Oystercatchers, at least in the short term, given that this study is just reflecting the instant intake by kleptoparasitism (i.e. the time scale is shorter than a complete feeding cycle). When analysing the potential costs and benefits of kleptoparasitism on a broader temporal scale, it should be considered that both resources are not equally predictable in time. Whereas Oystercatchers are regularly present in the intertidal zone feeding on clams (although in lower numbers than Coots), Coots were observed only sporadically and then in deeper water, feeding on crabs (G. O. García, pers. obs.). This difference in abundance and temporal predictability of both hosts as a resource for kleptoparasites, could be the cause of the regular presence of Gulls associated with Oystercatchers even though they are a less profitable in the short term. We suggest that future work should examine in more detail the costs and benefits for kleptoparasites with multiple hosts in similar systems elsewhere.

Acknowledgements

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