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Kleptoparasitism in wintering grey heron *Ardea cinerea*

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A b s t r a c t. Eighty-six cases of kleptoparasitism in grey herons, most of which were intraspecific, were observed in northern Spain and southwest France during four winters (1992-1995). Herons more often attacked individually than in groups, but the success was similar in both cases. Robbing success was significantly higher when herons attacked a young bird (44.4%) compared to adults (17.6%). Adult herons were significantly more successful (37.5%) than young herons (10.0%). Handling time had a great effect on the size of the prey item robbed by the herons. Adult herons were more frequently attacked by both young and adult birds. Age-related differences in winter foraging parameters (total time foraging, feeding success and biomass intake) may favour discrimination between victim age classes by kleptoparasites. Adult heron ingested 0.82 g min^{-1} during the winter season and young heron 0.45 g min^{-1}. For kleptoparasites adult herons seems to be a more profitable species than young. Kleptoparasitism increased the biomass intake of the pirate (62.8 g more than the normal intake of a young heron), probably to compensate for the inefficiency of young birds.

Key words: age, feeding parameters, handling time, robbery attempts

Introduction

Many articles have dealt with kleptoparasitism in birds, mainly in skuas, gulls, waders and terns (C a l d w e l l 1980, B u r g e r & G o c h f e l d 1981, T h o m p s o n 1983, 1986, H o c k e y et al. 1989, A m a t & A g u i l e r a 1990). Most of this work has focused on interspecific kleptoparasitism and much less attention has been paid to food stealing by conspecifics. Kleptoparasitism typically takes place where captured prey are clearly visible. Only a few studies have paid attention to this feeding behaviour in ardeids, while I am aware of only one study in the grey heron, *Ardea cinerea* (D u n b r a c k 1979, A m a t & A g u i l e r a 1989, 1990, V o i s i n 1991).

Several factors seem to influence the use of this feeding strategy, including the age of the birds involved, the size and shape of the prey and the number of pirates. The greater skill of adult birds in capturing prey (O r i a n s 1969, V e r b e e k 1977a, Q u i n n e y & S m i t h 1980, L e k u o n a 1997) may lead to them being attacked more frequently as the kleptoparasites' chance of success is higher (C a r r o l l & C r a m e r 1985, T h e r s h y et al. 1990), although in some cases there has been no evidence for this (V e r b e e k 1977b). Successful robberies increase with the age of the attacker (B u r g e r & G o c h f e l d 1979, H e p s & B a r n a r d 1989). Prey size has been related to the frequency of attacks, in that the larger the prey item captured by the host, the more attacks will be made (H u l s m a n 1976, B r o c k m a n n & B a r n a r d 1979). D u n n (1973) observed that smaller prey are attacked more frequently than larger and H u l s m a n (1984) mentioned the width and shape of the prey as important factors. Also, pirates may choose a specific prey length (some prey sizes are often rejected) or the most profitable prey (different prey species of the same size contain more or less energy) (D u n n 1973, Thompson 1986). Furthermore, Amat & Aguilera (1990) confirmed that several parasites attacking together robbed food more frequently than when individual attacks were made.

The numbers of grey herons wintering in northern Spain have increased over the past few years (Lekuona & Campos 1996a), resulting in an increased number of foraging birds at the feeding sites and the number of cases of kleptoparasitism (pers. observation). In this paper we present data on the influence of age and prey size on the success of kleptoparasitic behaviour in grey herons. We discuss the possibilities that kleptoparasitism is a profitable decision of dominant birds (adults), or an opportunistic behaviour shown by non-dominant birds (young).

Study Area, Material and Methods

The area under study includes the north of Spain (province of Navarra) and the southwest of France (the Orx lagoon and the Atlantic coast at Arcachon). Observations of foraging grey herons were made 2-3 days a week, from dawn until dusk, using 20-60x telescopes, at a distance <50 m. Visits were made to coastal bays, inland lakes, fish farms and reservoirs. The study was carried out over the period October-March during four years (1992-1995). We recorded: 1) species and age (adult or young birds, following the criteria of Cramp & Simmons 1977) of parasites and hosts, 2) the outcome of the robbery attempts (success if the kleptoparasite managed to catch the prey, failure if it did not manage to do so, even if the victim lost the prey), 3) the number of parasites participating in each attempt, 4) the relative size of the prey item captured in five size classes judged, in relation to the length of the bird's bill (Cramp & Simmons 1977), to be roughly (<8cm, 8-14 cm, 15-21 cm, 22-28 cm and >28cm).

The following data of winter foraging parameters were recorded: a) foraging time (Ft, min) as the total time spent at the feeding sites, from the time each heron arrived until it stopped foraging, b) number of feeding attempts and apparent result (success or failure). Foraging success was defined as the number of successful attempts dived by the total number of attempts, c) size and species of the fish captured. Mean biomass (g wet weight) of each prey item calculated from Arne's (1938), Richner's (1986) and Lekuona & Campos's (1996b) equations. Handling time was defined as the time it took between capturing and swallowing the prey. Next for each foraging bout, food intake rate (g fish min^{-1}) was computed by dividing biomass intake by Ft. A foraging bout was defined as the duration of an individual staying at the same feeding site without kleptoparasitic attacks. Foraging bouts were made in the same areas where kleptoparasitic attacks were observed. Mean robbed biomass was calculated taking into account the mean interval value of each prey size class .

All data were treated as one set of data because the number of kleptoparasitic attacks recorded in each year of study and at feeding sites was very low. Secondary robberies made by herons were included in the set data as a new attack. Unless otherwise stated, the data on successful attempts, size of prey robbed, age, number of attacks and number of parasites have been compared using the χ^2-test, with Yates correction when necessary (Sokal & Rohlf 1979). Foraging time (non-parametric data) have been compared using the Mann-Whitney Z test, and biomass intake (parametric data) with Student's t test. Handling time and prey size classes were tested with the Spearman rank coefficient (r_s).

Results

Description of the attacks

Both individual and group attacks were generally made from the ground, with birds approaching their victim on foot with their feathers ruffled, their bills open and their wings half spread. Hosts defended themselves either by facing up to the attacker or by flying away with the prey in their bills. When kleptoparasitic groups attacked one victim, usually one bird started it while the rest are followers. Often the leading grey heron got the prey and followers did not benefit. Sometimes followers made a secondary attempt to steal the prey from the leading heron.

Most of the attacks made by grey herons were intraspecific (Table 1). Some attacks were made on cormorant (*Phalacrocorax carbo*) and little egret (*Egretta garzetta*). No differences were found between intra- and interspecific robbery success (χ^2_1=0.1, n.s.). The herons more frequently attacked individually than in groups (83.7% and 16.3%, respectively, n=86, χ^2_1=326.4, p<0.01). There were no differences between the robbing success between group and individual attacks (χ^2_1=0.2, n.s.) (Table 1). The average size (±SD) of the kleptoparasitic groups was 2.3±0.6 birds (n=14). In such groups young birds were dominant (78.1% compared with 21.9% adults, n=32).

Winter food

In the area under study, grey heron was basically piscivorous (L e k u o n a 1 997). During winter the main prey species caught by herons were eel (*Anguilla anguilla*), thick-lipped grey mullet (*Chelon labrosus*), flounder (*Pleurenectes flesus*), carp (*Cyprinus carpio*), barbel (*Barbus*

Table 1. Number (n) of kleptoparasitic attempts made by grey herons individually and in groups and the corresponding success rates.

	Individually		In groups		Total	
Victim	n	% success	n	% success	n	% success
Grey heron	65	27.7	13	23.1	78	26.9
Cormorant	1	-	1	-	2	-
Other species	6	50.0	-	-	6	50.0
Total	72	29.2	14	21.4	86	27.9

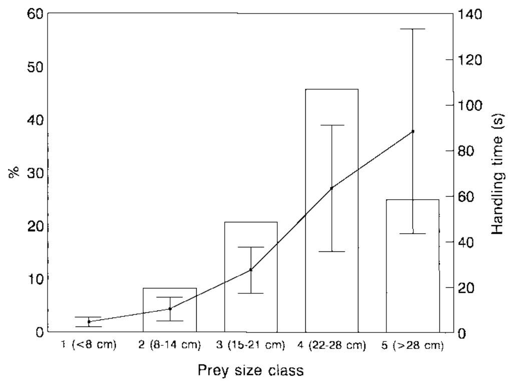

Fig. 1. Percentage of prey items robbed (bars, left axis) by herons and average (± SD) handling time (line, right axis) in relation to prey size (cm).

graellsii) and French nase (*Chondrostoma miegii*). Twenty-four fishes were stolen by grey heron during the study period: 37.5% were flounders, 33.3% carps, 16.6% barbels and 12.5% eels.

Influence of fish size

The size of 24 stolen prey items could be recorded (3 from group attacks and 21 from individual attacks). As a result of the small sample size it is not possible to calculate the differences between the two modes of attack. Most prey items were size class 4 (eel, flounder and carp, mainly), and none was smaller than size class 2 (Fig. 1). The frequency of stolen prey items increased with handling time, except for prey items size class 5 (Fig. 1). There was found a relation between the prey size classes stolen by herons (2, 3 and 4) and their respective handling time (Spearman, r_s=0.99, p<0.01). Handling times longer than 5 seconds increased the probability of attacks.

Influence of age

Adult grey herons made more robbery attempts (χ^2_1=28.5, p<0.001) and were significantly more successful (37.5%) than young herons (10.0%) (χ^2_1=12.4, p<0.01) (Table 2). Robbing success was significantly higher when herons attacked a young bird (44.4%) compared to adults (17.6%) (χ^2_1=6.8, p<0.01).

No differences were found between age-victims attacked by adult herons (χ^2_1=2.4, n.s). Young herons made more robbery attacks on adults than on young victims (χ^2_1=4.8, p<0.05). In the overall data, adult herons were attacked more frequently than young birds (χ^2_1=6.8, p<0.01). Adult and young herons were not attacked at a higher frequency than that at which they were encountered in the wintering population (χ^2_1=0.6, n.s.) (60.3% were adults (n=1209, Lekuona & Campos 1996a).

When adult birds were attacked they lost significantly fewer prey items than young birds did (χ^2_1=27.2, p<0.001).

Winter feeding parameters

In 71 feeding bouts the age of birds was recorded (Table 3). Adult herons spent less time foraging than young birds (Mann-Whitney Z test, Z=4.81, p<0.001). The frequency of successfull attempts made by adult herons was higher than by young (χ^2_1=24.6, p<0.001). The estimated biomass intake of adult herons was higher than that of young birds (Student t test, t=3.6, p<0.001). When foraging efficiency is expressed in terms of biomass, adult heron ingested 0.82 g min^{-1} during the winter season and young heron 0.45 g min^{-1}. For pirates, adult herons seems to be a more profitable species than young herons.

In few cases (20%, n=25) the kleptoparasitic behaviour was recorded when young herons fed actively (with low foraging success) and other feeding herons were in the proximity. After the robbery attack the controlled bird continued feeding at the same foraging area. Kleptoparasitism increased the biomass intake (as average±SD) of the pirate by 62.8±36.8 g (n=24) more than the normal intake of a young heron (230.5±58.9, n=25); Student t test, t=3.8, p<0.001), probably to compensate the inefficiency of young birds.

Discussion

Grey heron attacked as individuals rather than in groups when stealing prey. This indicates that the frequency of kleptoparasitism is more a reflection of the social structure than a test of a density-dependent phenomenon, as was suggested by Krebs & Barnard (1980).

Table 2. Number (n) of kleptoparasitic attempts made by grey heron according to age and corresponding success rates.

	Kleptoparasite					
	Adult		Young		Total	
Victim	n	% success	n	% success	n	% success
Adult grey heron	31	22.6	20	10.0	51	17.6
Young grey heron	19	57.9	8	12.5	27	44.4
Other species	6	50.0	2	-	8	37.5
Total	56	37.5	30	10.0	86	27.9

Table 3. Foraging parameters of adult and young grey herons during the wintering season. N: number of foraging bouts, A: number of attempts, S: % of success, Ft: foraging time (in minutes), B: biomass taken (in g). Ft and B as average±SD.

Age	N	A	S	Ft	B
Adult	46	410	74.3	281.8±32.3	232.0±91.3
Young	25	267	59.3	368.2±61.1	165.7±38.9

This may be due to the low numbers of birds in the area under study (pers. obs.) or to the fact that most birds defend a territory when they forage (Richner 1986), thus making it difficult for two or more birds to be close together.

Group attacks did not provide a higher success than those of individual birds. Kleptoparasites within a group did not share the prey, so the benefit per bird diminished with increasing group size. The winter feeding success of young herons was lower than that of adults, which might favour the formation of kleptoparasitic groups, thus compensating for their lack of experience in the search and detection of prey. Also, young herons could make kleptoparasitic groups in the winter feeding areas for stealing abandoned prey from another young.

Handling times have a great influence on the selection of the prey items stolen by the grey heron, and it appears that in this species the size of the prey is an important factor in kleptoparasitism, as has been proposed by Dunbrack (1979), Ens et al. (1990) and Amat & Aguilera (1990) for other species.

Adult herons were more frequently attacked than young birds and they were the main victim for young herons. Therefore, this suggests that grey heron did not show selection for victims. There were more adults in the observed population (Lekuona & Campos 1996a), so kleptoparasitic attempts were just done on an opportunistic behaviour and as a result of the greater foraging success and higher foraging efficiency of adult birds. Both adult and young herons concentrate their kleptoparasitism on the age-class that is likely to be more profitable (adult herons). Young herons need to consider the trade-off between attacking adult birds (higher biomass intake) and the risk (adult grey herons respond very aggressively to kleptoparasitic birds). These age-related differences may favour discrimination between victim age classes by kleptoparasites. These results suggest the need of additional studies of kleptoparasitism focusing on the overall rate of victim choice and rate of attacks of each age class in grey herons.

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