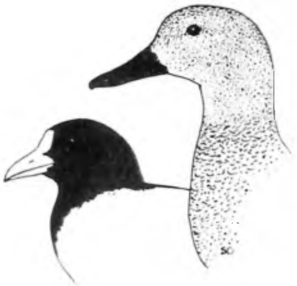
# Food usurpation by waterfowl and waders



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*Both waterfowl and waders typically aggregate in mixed-species foraging flocks. When foraging, individuals in groups can use the information provided by other individuals, so that they can copy the foraging modes and/or locations or even steal the food previously procured by the other individuals. The prevalence of feeding by scrounging by waterfowl and waders varies in association with some factors which make more or less likely the occurrence of scroungers when individuals of these groups forage in flocks. When food requires short handling times and is clumped in patches, there is the possibility of the development of imitative (copying) foraging tactics; when food requires longer handling times, there is possibility for a more exploitative foraging tactic (kleptoparasitism). In between these two situations other cases may occur, such as supplanting from feeding sites. The usurpation of food, either directly (kleptoparasitism) or indirectly (copying, supplanting), may have some impact on the rates of food intake of usurped individuals. To reduce such impact, usurped individuals may adopt behavioural strategies. As these strategies might be costly, there would be some tradeoff between their adoption and feeding efficiency.*

A common aspect of the ecology of both waterfowl and waders is that, during the non-breeding season, they aggregate in flocks that may be composed of thousands of individuals (e.g. Mercier & Gaskin 1985). One of the major hypothetical advantages of flocking in birds is an increase in feeding rate, due either to a reduced proportion of time spent being vigilant for predators or to an improvement in feeding efficiency (from local enhancement, reduced duplication of searching effort, formation of search images, cooperative hunting, etc.). However, there are also costs to being in a flock, mainly due to mutual interference while foraging, as well as interactions such as aggression between individuals (see e.g. Herrera 1979, Barnard & Thompson 1985).

One way of reducing costs associated with food-finding is to allow other individuals to find the food and then to usurp them, either directly (that is, by kleptoparasitism), or indirectly (that is, by copying the foraging sites or feeding behaviour of other individuals, or by supplanting other individuals from feeding sites) (Barnard 1984). To copy others may not always be usurping; however, this foraging mode mainly occurs when food presents a patchy distribution, and in these circumstances an individual's feeding intake rate may be negatively affected by the number of individuals attracted to the feeding site. Thus, although food finding may be more efficient for birds in a flock as a result of copying others (Krebs *et al.* 1972), this could also have the disadvantage of increasing travelling times between patches as a result of depleting the food within a patch more quickly. Therefore, under these circumstances copying may be considered as an indirect form of food usurpation.

In this review I will first focus on cases of food usurpation in waterfowl and waders, namely copying, supplanting and kleptoparasitism. Second, I will discuss on the prevalence of these feeding tactics, paying attention to those ecological factors which could influence the incidence of scroungers when individuals of both groups forage in flocks. Finally, I will comment on the behavioural strategies adopted by waterfowl and waders to reduce the impact of food usurpation.

## Occurrence of foraging by scrounging

### *Copying*

The opportunities for animals to adopt a novel behaviour as a result of observing others per-

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forming it (what has been termed social learning, imitation, copying, etc.) should be particularly common in group-living individuals, since the opportunities for it would increase with increasing contact between them (see Giraldeau & Lefebvre 1987).

Social learning may result from some individuals following others to a general area where food is abundant (i.e. from local enhancement), but once there they feed independently of the other individuals. I will not consider this behaviour here. Local enhancement has been experimentally demonstrated for Barnacle Geese *Branta leucopsis* (Drent & Swierstra 1977, Zhu *et al.* 1987), Brent Geese *Branta bernicla* (Inglis & Isaacson 1978), Goosander *Mergus merganser* (Wood 1985) and waders (Gerstenberg & Harris 1976). In the studies of geese it was found that the probability of flying birds landing at a site was greater when geese models positioned at the site were in a grazing posture than when they were in alert posture. Similarly, Smew *Mergus albellus* were attracted to sites where large flocks of conspecifics were diving for food (Beintema 1980), as were Dunlin *Calidris alpina* in tidal areas where Mallard *Anas platyrhynchos* were feeding (Thompson *et al.* 1986).

There is another mechanism from which social learning may result: when individuals forage in flocks in a particular area they may be mutually observing each other, and may quickly change behaviour depending on what other individuals are doing, to capitalize on short term changes in food availability. In interspecific associations, copying others could lead to the exploitation of new feeding sites or even resources (Barnard 1984).

One difficulty in studying the impact of copying on both copied and copying birds is that intake rates are not usually easy to quantify. Furthermore, in many instances copying may be a rather subtle behaviour, so that it may be difficult to detect. Perhaps because of these reasons, at present there are few studies dealing with copying in waterfowl and waders. Recently, however, there have been a number of papers whose results suggest that copying may have an important effect on flock dynamics and habitat use, as well as on the composition of interspecific foraging assemblages.

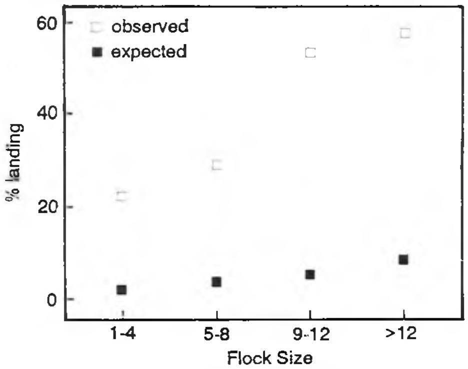

**Figure 1. Expected and observed percentages of occasions when Green-winged Teal landed at a distance of <3 m from foraging conspecifics, for different flock sizes.** Modified after Pöysä (1987).

For Green-winged Teal *Anas crecca* it has been shown that the proportion of individuals landing less than 3 m from a foraging conspecific was greater than expected (Fig. 1). Furthermore, there was evidence that when starting to forage, newly-arrived birds did not respond to feeding conditions at the landing site *per se*, but instead copied the feeding methods of the individuals already present. In this way, Teals would reduce the time needed to search for food upon arrival at a site (Pöysä 1987).

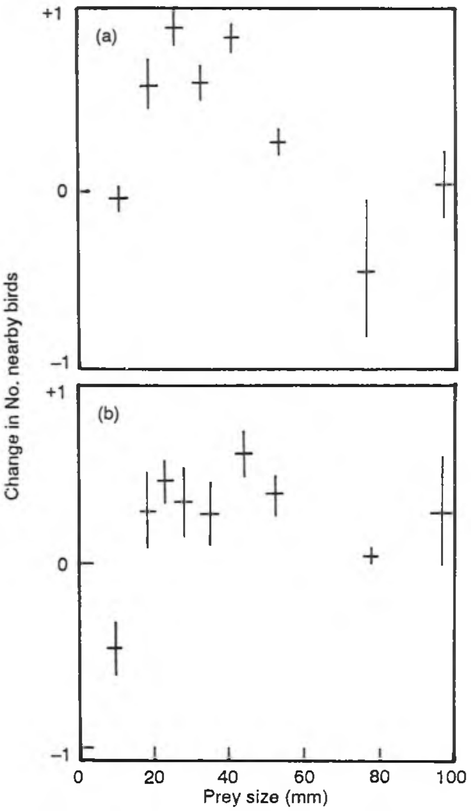

**Figure 2. Changes in the mean number (± s.e.) of Lapwings and Golden Plovers within 2-3 m of a successful (a) plover and (b) lapwing, respectively, in the 20 second period following prey capture, in relation to prey size.** Modified after Barnard *et al.* (1982).

In mixed-species foraging groups of Lapwings *Vanellus vanellus* and Golden Plovers *Pluvialis apricaria* the number of heterospecifics within 2-3 m of focal birds changed in relation to the size of the worm captured by the focal bird (Fig. 2). There was a tendency for birds to accumulate around successful heterospecifics, but mainly when worms captured were between 20-40 mm, which were those most profitable to both plover species (Barnard *et al.* 1982).

The situation in heterospecific groups of Crowned *Vanellus coronatus* and Black-winged Plovers *Vanellus melanopterus* was different. When a member of either species found a patch of high prey density, it was immediately joined by all other members of the mixed flock. Therefore, feeding rates could be enhanced in a flock because each bird might capitalize on patches of high prey density that it might not necessarily have found itself or might have taken longer to find (Ward & Maclean 1988).

Neither of the previously mentioned studies, however, identified costs and benefits (in terms of feeding intake rates) for the participants in these feeding interactions. The food intake rate of Gadwall *Anas strepera* copying the foraging sites of Coot *Fulica atra* was similar to that of individuals that did not copy, but copying Gadwall used less costly foraging methods. The intake rate of Coot was somewhat depressed because of copying (J.A. Amat & J.R. Obeso unpubl.).

### *Supplanting*

Although supplanting from foraging sites is easier to observe than copying, it has also received little attention, and most reported cases are anecdotal. At an intraspecific level, it has been recorded for White-fronted Geese *Anser albifrons* foraging in small snow-free patches of grass (Boyd 1953), Canada Geese *Branta canadensis* on baited sites or where food was concentrated (Hanson 1953, Raveling 1970), Greylag Geese *Anser anser* foraging on *Scirpus* tubers under conditions of food scarcity (Amat 1986), American Wigeon *Anas americana* displacing each other from the nearest position to foraging coot in order to kleptoparasitize them (Knapton & Knudsen 1978), and Oystercatchers *Haematopus ostralegus*, Turnstones *Arenaria interpres*, Purple Sandpipers *Calidris maritima* and Short-billed Dowitchers *Limnodromus griseus*, among other wader species, foraging on patchily distributed invertebrates (Mallory & Schneider 1979, Vines 1980, Fleischer 1983, Metcalfe 1986, Sullivan 1986). In most of these studies only the outcome and/or motivation of attacks was recorded, but no information was presented on intake rates.

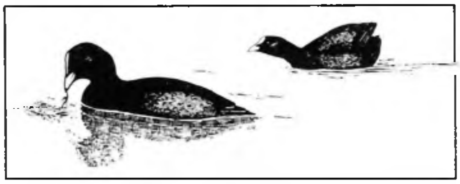

**Figure 3. A Coot approaching another to supplant it from a feeding site; drawing by J. López-Rojas.**

By supplanting conspecifics, Coots (Fig. 3) did not increase the amount of food ingested relative to birds feeding conventionally (Fig. 4), but instead reduced the costs associated with obtaining food, since they spent less time foraging by the more costly method, and also improved their searching efficiency, since after supplanting they obtained the same amount of food plants from each foraging attempt, but had shorter dive durations. The rate of food intake of supplanted Coots was lower than that of unmolested birds (Fig. 4), despite both groups of Coot diving with similar frequency, indicating that supplanted Coots were displaced to sites of lower quality (Amat & Obeso 1989).

Although supplanting has also been recorded at an interspecific level, there are no studies specifically dealing with this feeding behaviour. It has been observed among ducks of different species feeding in association with swans (Bai-

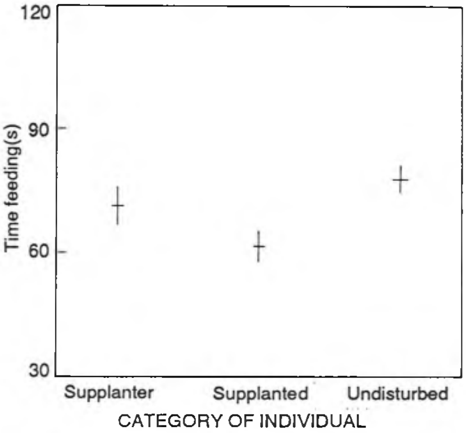

**Figure 4. Mean time (± s.e.) during a 2 minute observation period that Coots spent foraging on plants brought to the water surface after diving.** The data are divided into Coot that supplanted others, those that were supplanted, and those that were not disturbed during the 2 minute period. Differences were only significant between supplanted and undisturbed birds ($t = 2.35, P<0.05$, for log-transformed data). After Amat & Obeso (1989).

ley & Batt 1974), in which the ducks displaced one another from the nearest position to the feeding swan in order to remove waste particles from vegetation taken up by swans. For waders, supplanting among heterospecifics is less frequent than among conspecifics (e.g. Burger *et al.* 1979, Wishart & Sealy 1980, Metcalfe & Furness 1987). Slatey Egrets *Egretta vinaceigula* were recorded chasing Greenshanks *Tringa nebularia* away from feeding sites (Mathews & McQuaid 1983). Coots have occasionally been observed displacing herbivorous diving ducks from foraging sites (pers. obs.).

### *Kleptoparasitism*

Kleptoparasitism is a more direct and easily observable foraging interaction than copying and supplanting. Perhaps for this reason, there are several well detailed studies in which waterfowl or waders are involved, either as pirates and/or hosts of kleptoparasitic interactions.

Waterfowl are victims of gulls and raptors, although food stealing between members of this group has also been recorded; ducks have been recorded robbing other ducks as well as swans and coots (Brockmann & Barnard 1979). Intraspecific kleptoparasitism among ducks has also been recorded (Harper 1982, Woodall 1984, Wood 1985); for wild geese it has only been observed between Greylags (Amat 1986), though attempts of food stealing have also been recorded for the Snow Goose *Anser caerulescens* (Jenkins 1944).

Waders are mainly victims of gulls, but also of other waders; as pirates, they have been recorded kleptoparasitizing other waders and rarely gulls (Stenzel *et al.* 1976, Brockmann & Barnard 1979, Barnard & Thompson 1985, Ferns in press). Intraspecific food stealing has been observed in some species, e.g. Oystercatcher (Vines 1980, Goss-Custard *et al.* 1982), Turnstone (Metcalfe 1986), Lapwing and Golden Plover (Barnard & Thompson 1985), Ringed Plover *Charadrius hiaticula* (Ferns in press), Dunlin (Payne & Howe 1976), and Curlew (Ens *et al.* 1990).

Several studies have established the costs and benefits for the participants in the kleptoparasitic interactions. Gulls robbing plovers were probably able to meet daily energy requirements solely by robbing (Källander 1977); as a consequence of the kleptoparasitic activities of the gulls, the plovers were forced to leave the feeding site or had to spend longer feeding to compensate for food losses (Barnard & Thompson 1985). Only dominant Oystercatchers increased their rate of food intake by stealing from conspecifics, while subordinates had to use suboptimal areas (Goss-Custard *et al.* 1982, see also Metcalfe 1986). Curlews significantly increased intake rate by robbing conspecifics (Ens *et al.* 1990). Gadwalls kleptoparasitizing Coots did not increase their rate of food intake relative to birds feeding conventionally, but they used less costly foraging methods; parasitized Coots had the same rate of food intake as unparasitized individuals, but they maintained this by diving more often (Amat & Soriguer 1984).

## Factors favouring the occurrence of foraging by scrounging

### *Food type and distribution*

There are several factors that may favour the occurrence of scrounging interactions when waterfowl and waders forage in flocks. Some of these are mainly related to both food type and distribution, as well as concentration of individuals (Brockmann & Barnard 1979, Barnard 1984), and are discussed below for each particular situation.

The nature of the food is important in explaining the prevailing type of interaction. When (a) limited resources are found in dispersed, rich patches, (b) these resources also require short handling times before ingestion, and/or (c) the defence of the site is costly, imitative foraging tactics may develop. When food requires longer handling times, more exploitative foraging tactics are possible, such as kleptoparasitism. In between these two extremes supplanting from foraging sites may occur.

The concentration of individuals while foraging may increase competition through either interference, food depletion, or both. To offset this, individuals may space out. When foraging, waders vary in their degree of dispersion from compact to widely dispersed (Goss-Custard 1970, Myers 1984); in waterfowl, foraging flocks vary from dense packing to wider spacing (Zwarts 1976, Johnson & Raveling 1988). The degree of compactness depends on whether or not foraging efficiency is depressed by compact flocking (Recher & Recher 1969, Goss-Custard 1970, Burger *et al.* 1979, Myers 1984).

### *Copying*

When prey items are of small size or poor nutritive quality, individuals may be under pressure to optimize feeding time and minimize time spent in agonistic interactions. This conflict may be exacerbated in tidal areas because of the effects of tides in limiting foraging time. In these situations, individuals might forage in compact flocks when resources are concentrated in patches, and this could lead to the utilization of imitative foraging tactics, unless food availability being depleted by bird activity (e.g. Selman & Goss-Custard 1988). When waders feed on extremely dense aggregation of prey, they suppress aggression (Recher & Recher 1969, Puttick 1981, Stawarczyk 1984). As waders foraging by tactile probing require less feeding space than visual foragers, and exhibit lower rates of aggression (Recher & Recher 1969, Goss-Custard 1977, Burger *et al.* 1979), the opportunities for copying should be higher for tactile than for visual forager species. Although the imitative behaviour is probably more frequent at an intraspecific level, the opportunities for interspecific copying in mixed-species flocks of both waterfowl and waders may be high. Waders may use similar feeding areas and foraging behaviours, and also can exhibit a high degree of dietary overlap (Baker 1977, Goss-Custard *et al.* 1977, Pienkowski 1978/79, Stawarczyk 1984). Waterfowl may also use similar areas and several, not species-specific, foraging behaviours depending on water levels (Szijj 1965, Thomas 1982, Pöysä 1986).

There are probably other factors, such as the detectability of the food and the likelihood of it being depleted, which may also predispose individuals to copy others. By copying the foraging sites of others, an individual can capitalize on the availability of a rich, probably rapidly depleting food supply (as in Crowned and Black-winged Plovers, Ward & Maclean 1988). The foraging behaviour exhibited by an individual can indicate how to gain access to the food supply, and by copying it another individual could greatly reduce searching times (as in Green-winged Teal, Pöysä 1987).

### *Supplanting*

If food items are distributed in discrete patches of small size, there may be differences in foraging success between individuals. In this case, it may be advantageous to defend patches against the intrusion of others and in this situation a way of increasing intake rates should be by displacing other individuals from the feeding sites. Indeed, Fleischer (1983) found that when foraging success decreased, supplanting rate between Turnstones increased. The quality of resources may also affect the frequency of supplanting, which should be higher when resources are of high quality (Johnson 1989), or when in spite of being of lower quality, they are concentrated in these patches in such quantity that it may be advantageous to supplant others, since in this way food intake may increase and/or searching time may be reduced (as in some waders and Coot, Recher & Recher 1969, Mallory & Schneider 1979, Amat & Obeso 1989).

Supplanting may entail some costs for the supplanter individual, as an agonistic interaction is required, and it should be expected that the more valuable the resource, the stronger its defence by the owner (cf. Rubenstein 1981). Because of this, the supplanter should assess, before the contest, the value of the site it will attempt to obtain. In this context, it can be argued that supplanting should be more frequent in visual than in tactile feeding waders, and in waterfowl feeding in shallow than in those feeding in deep waters. The reason may be that individuals foraging on prey located near the surface can provide others with information about their foraging success, and in turn about the quality of the feeding site. In contrast, when individuals forage on prey that are distributed more deeply, their food intake rates should be more difficult to estimate if prey are consumed below the surface; in this group of species, supplanting should be more frequent when they make visible their prey by bringing them to the surface to consume (e.g. Coot, some ducks).

### *Kleptoparasitism*

One of the main factors making waterfowl and waders vulnerable to kleptoparasitism is the long handling time of some of their prey (Brockmann & Barnard 1979). Intraspecific kleptoparasitism has been recorded in some waterfowl and waders (see above). Interspecific food-stealing has been recorded in at least 558 pair species of birds (J.A. Amat in prep.). As victims, waterfowl (anatids and coots) were involved in 69 (12.4%), and waders in 55 (9.9%) of such cases. As pirates, waterfowl were recorded in 19 (3.4%), and waders in 21 (3.8%) of the 558 cases. Waterfowl, especially the diving species, often bring large food items to the water surface to eat them there, so making food available to pirates, which are usually species feeding shallower than hosts (e.g. Söding 1950, Knapton & Knudsen 1978, Grace 1980, Woodall 1984, Eddleman *et al.* 1985). When food is of low nutritive quality, some waterfowl species would kleptoparasitize others to reduce costs associated with obtaining it (Amat & Soriguer 1984).

### *Asymmetries in dominance*

When individuals contest over resources, asymmetries in dominance may be important in determining the outcome of foraging interactions. Since the intensity of interactions escalates from copying to kleptoparasitism in relation to the value of the resources, relative dominance should become more important in determining the outcome in kleptoparasitic than in copying interactions (cf. Rubenstein 1981), unless birds steal food using methods which do not require superior force (e.g. pilfering and peculation; see Vollrath 1984). However, in waterfowl and waders the opportunities for the latter are practically non-existent (J.A. Amat in prep.).

It has been shown both in intra- and in interspecific cases of supplanting and kleptoparasitism that birds that displace or steal food from others are usually dominant, either because of their larger size, or by being more aggressive or numerous (Boyd 1953, Hanson 1953, Recher & Recher 1969, Bailey & Batt 1974, Burger *et al.* 1979, Vines 1980, Harper 1982, Stawarczyk 1984, Metcalfe 1986, Metcalfe & Furness 1987, Ens *et al.* 1990). However, this need not always be the case, in some circumstances it may not be profitable for usurped individuals to retaliate against their attacker (regardless of their relative dominance status) since this would further reduce their intake rate (Amat & Soriguer 1984, Sullivan 1986).

When defending a resource results in a lowered food intake rate, as in many copying and some supplanting and kleptoparasitic situations, there is an opportunity for individuals to participate in scrounging regardless of their dominance status. Thus, of the usurpation feeding tactics, copying would be the one mainly explaining the adaptiveness of feeding by scrounging for low ranking individuals (Waite & Grubb 1988).

## Behavioural strategies to reduce impacts of scroungers

When individuals forage in groups, the opportunity exists for some of them to pay attention to the activities of others, so gaining information about their foraging success, and consequently about the best feeding situations (Barnard 1984). Gadwalls seemed to pay attention to the activities of Coots, mainly copying those that brought the largest quantities of food plants to the water surface (and were therefore probably in the best sites) (J.A. Amat & J.R. Obeso unpubl.). When kleptoparasitic gulls attended several wader species, they attacked preferentially those with which the highest foraging gains were attained (Thompson 1986, Amat & Aguilera 1990). Gadwalls mainly kleptoparasitized those Coots with lower diving rates, suggesting that the ducks avoided parasitizing the Coots which brought small quantities of plants to the surface (Amat & Soriguer 1984).

These observations suggest that the impact of scroungers may be more severe on individuals with highest rates of food intake and/or on those feeding in sites of better quality. To reduce this impact, usurped individuals may adopt several strategies: retaliation, toleration/compensation, and evasion (Barnard 1984).

Retaliation has been observed rarely among waterfowl (e.g. Amat & Soriguer 1984, Amat 1986, Bergan & Smith 1986) or waders (e.g. Vines 1980, Ens *et al.* 1990). In spite of being more aggressive than Gadwall, Coots tolerate the kleptoparasitism of ducks and compensate for this by diving more frequently (Ryan 1981, Amat & Soriguer 1984). Evasion (usually against kleptoparasites) is the most frequent strategy adopted to reduce food loss; several evasive tactics have been observed: victims may (1) synchronize activities to confuse kleptoparasites (e.g. seaducks attended by gulls, Schenkeveld & Ydenberg 1985), (2) handle prey faster (e.g. plovers attended by gulls, Barnard & Thompson 1985), (3) increase their distance from pirates (e.g. Coot parasitized by Gadwall, plovers by gulls, and both Oystercatchers and Curlews by conspecifics, Vines 1980, Ryan 1981, Thompson 1986, Ens *et al.* 1990), (4) shift to a less vulnerable diet (e.g. when plovers are attended by gulls, Thompson & Barnard 1984), or (5) keep their prey out of the kleptoparasite's sight (as plovers and godwits attended by gulls, Thompson 1986, Amat & Aguilera 1989).

Although evasive actions may reduce the likelihood of food usurpation (Thompson 1986, Amat & Aguilera 1989), they may lead to loss of feeding time or a shift to lower quality diets, and thus they may be costly. For this reason, tradeoffs related to food usurpation are likely to be important in determining whether strategies reducing the impact of scroungers are adopted. There is some evidence for this: Hesp & Barnard (1989) showed that immature gulls were less successful at stealing worms (Lumbricidae) from Lapwings than were adults, and suggested that, to compensate for this, young gulls should increase their attack rate thus causing more frequent disturbance to the Lapwings. These authors predicted that Lapwings should reduce their vulnerability to attack by moving away more frequently when an immature landed close to them than when an adult did so, a prediction that was partially fulfilled.

If the attack is not avoided, the host may still be reluctant to relinquish prey to the kleptoparasite, even if pursued. The most frequent type of pursuit is aerial, though running and underwater pursuits have also been observed (Anderson *et al.* 1974, Brockmann & Barnard 1979, Grace 1980, Woodall 1984). The reluctance to drop the prey item should be higher in more manoeuvrable host species that are more likely to escape (Thompson 1986, Amat & Aguilera 1990), or in those with lower feeding success (Barnard 1984, Amat & Aguilera 1989); individual Black-tailed Godwits *Limosa limosa* with lower rates of prey capture were slower to relinquish their prey to kleptoparasitic gulls than individuals with higher capture rates (Fig. 5). However, hosts will quickly drop the prey if there is little opportunity to escape.

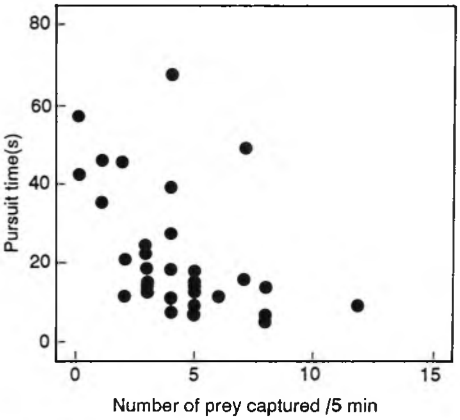

**Figure 5. Relationship between the duration of chases of Black-tailed Godwits by Black-headed Gulls and the foraging success of the chased bird, considered as the number of prey captured during a 5 minute period immediately after the chase ($r = -0.59$, $P<0.01$, for log $(x + 1)$-transformed data).** After E. Aguilera & J.A. Amat (unpubl.).

To summarize, the behavioural options of victims faced with the threat of food usurpation should depend on the relative costs and benefits of each option (Sullivan 1986, Ydenberg & Dill 1986). The relative cost of each option might be affected by the foraging efficiency of victims and their vulnerability to food usurpation (cf. Formanowicz & Brodie 1988).

## Concluding remarks

At present there is little quantitative observation on copying and supplanting interactions in the foraging of waterfowl and waders, although kleptoparasitism has been better studied. Consequently, much of the information gathered here cannot be used to test the predictions made. Any real understanding of the occurrence of usurpation foraging tactics requires, at least, a knowledge of their effect on the feeding intake rates of the participants in such feeding interactions, and how the latter are sensitive to food type and food distribution. Furthermore, the influence of vulnerability to food usurpation in the decision making process of victims may be of interest if there is some tradeoff between the adoption of tactics reducing vulnerability to food loss and feeding efficiency. It would be interesting also to know the influence that such tactics by hosts have on the persistence of scroungers in attending flocks.

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