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Interspecific kleptoparasitism by four species of gull *Larus* spp. in South Sweden

Iakttagelser i södra Sverige av fyra måsarters stöld av föda från andra arter

HANS KÄLLANDER

Abstract

Data are presented on interspecific kleptoparasitism by Black-headed Gull *Larus ridibundus*, Common Gull *L. canus*, Herring Gull *L. argentatus* and Great Black-backed Gull *L. marinus*, collected in South Sweden from the late 1950s to the present day. The basis for the presentation is the various host species exploited by the four gull species. For each host species, information is given on species of gull kleptoparasitising it, seasonal occurrence of kleptoparasitism, details of behaviour and, when available, data on gulls' success rates. The paper is intended as a sort of catalogue. For this reason, relevant literature is reviewed under each of the host-species headings. Gulls' success rates varied between 55% for Black-headed Gulls and Common Gulls parasitising Northern Lapwings *Vanellus vanellus*, the most often observed kleptoparasitic association, and 15% on the few occasions that Black-headed Gulls parasitised Curlews *Numenius arquata* in grassland. When the same two gull species parasitised Common Starlings *Sturnus vulgaris*, their success rate varied with robbing tactic used (16% vs 45%). Beside the association of the two small gull species with Lapwings and Golden Plovers *Pluvialis apricaria*, the most frequently observed associations were those of Herring Gulls with Common Eiders *Somateria mollissima* and Great Black-backed Gulls and Herring Gulls with diving fish-eaters (Great Cormorant *Phalacrocorax carbo*, mergansers *Mergus* spp.). Kleptoparasitism often occurred during periods of food scarcity, being most common in harsh winter conditions (the two large gull species) and during cold spells in early spring (some associations of the two small gull species). As in other studies, gulls' success rate was strongly dependent on the size of hosts' prey, and thus, normally on handling time. It is suggested that success rate can often be used as a substitute for profitability in studies of kleptoparasitism.

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Introduction

This paper presents data from South Sweden on interspecific kleptoparasitism, or food stealing, by four species of gull. The gull species treated are Black-headed Gull *Larus ridibundus*, Common Gull *L. canus*, Herring Gull *L. argentatus* and Great Black-backed Gull *L. marinus*. The paper is intended as a sort of catalogue, summarised in an Appendix. In the account below I take as a basis the various hosts exploited by one or more of the four gull species (but disregard cases of food robbery between the gull species), report on the seasonal occurrence of their kleptoparasitism, relate their behaviour to the hosts' foraging behaviour, describe the tactics used by the parasites to sequester food from the victims and the tactics these use to avoid losing their food. When available, data are also presented on the kleptoparasite's success rate, i.e. the proportion of attempted robbery resulting in the parasite obtaining the food. No complete litterature search has been done, but relevant references I have found are reviewed in each host-species section. No doubt many notes on kleptoparasitism by gulls are hidden in local and regional bird journals of limited circulation as well as in books.

From the late 1950s onwards I have collected data on kletoparasitism in connection with general bird-watching but data have also been gathered more systematically during certain periods. This applies particularly to studies of the association between the two smaller gull species and two species of plover, Northern Lapwing *Vanellus vanellus* and Golden Plover *Pluvialis apricaria*. Much time has also been devoted to the study of gulls' exploitation of diving, fish-eating birds.

Herring Gull attending feeding Whooper Swans.
Gråtrut som bevakar födosökande sångsvanar, Lomma, 19 februari 1964.

Sometimes the line between kleptoparasitism and commensalism is difficult to draw. A typical example of this is the widespread association between European Wigeon *Anas penelope* and Eurasian Coot *Fulica atra* (e.g., Söding 1950) and between American Wigeon *Anas americana* and American Coot *Fulica americana* (e.g., Knapton & Knudsen 1978). Coots dive and bring plant food to the surface, where it is consumed. Mostly wigeon only pick up plant fragments that the Coot ignores, i.e. commensalism. In other situations wigeon seize plants directly from the Coot's bill, i.e. kleptoparasitism. In still other situations a wigeon may pick up food from the water surface that the Coot may or may not have intended to consume. Another situation is when Common Gulls, and sometimes Black-headed Gulls, exploit some species of diving fish-eating birds, namely Great Cormorant *Phalacrocorax carbo*, mergansers *Mergus* spp. and Great Crested Grebe *Podiceps cristatus*. In addition to kleptoparasitic Great Black-backed Gulls and Herring Gulls, these flock-fishing species regularly attract one or both of the two smaller gull species, which circle above the fishing flocks and plunge-dive headlong among the birds. Most such dives no doubt are aimed at fish driven towards the surface by the activities of the diving species as indicated by the fact that the gulls may plunge-dive also some distance away from the latter. This use of the diving species clearly falls under the term commensalism. However, some dives may be directed at birds as these approach the surface with fish in the bill, something that is extremely difficult to verify. If they are, then they should be called attempts at kleptoparasitism.

Metods

The study is based on observation, sometimes (gull-plover association) from a car using 10x binoculars, in other situations without any hide and using 10x binoculars and/or a 20x or 20-60x spotting scope. Some observations were talked into a tape-recorder and later transcribed. Most data were collected in Skåne, the southernmost province of Sweden, but data also from other parts of South Sweden have been used.

It should be pointed out that values for success rate presented below suffer from varying degrees of pseudoreplication, something they have in common with most or all such data that have been presented in the literature. Avoiding recording more than one stealing attempt per individual kleptoparasite is impossible in practise because the number of parasites at a particular site is always limited. Since kleptoparasites are rarely individually recognisable, it is also not feasible to calculate a mean success rate for each individual. Despite this weakness, I am convinced that statistical differences in success rate between species of gull kleptoparasitising the same host as well as differences in success rate of one species exploiting different hosts give an accurate picture. Furthermore, one should keep in mind that the success of a kleptoparasite varies with the circumstances, in particular with the size and handling time of the prey taken by the host. For

that reason it would perhaps have been more appropriate to present ranges for success rates rather than means; nonetheless I have chosen the latter. P-values are for 2-tailed tests throughout.

In the following listing of the kleptoparasitic interactions recorded in this study, I use the new, official names of the host species when these are mentioned in the headings but, for simplicity, stick to the old names in the associated texts.

The hosts and the gull species kleptoparasitising them

Divers Gavia *spp.*

In South Sweden I have only made two observations of gulls (Great Black-backed Gull and Herring Gull) attending Black-throated Divers *Gavia arctica*. However, in the northernmost part of the Gulf of Bothnia, where large flocks of Black-throated Divers stop over in late May, I have recorded intense kleptoparasitism by Great Black-backed Gulls, Herring Gulls and, especially, Lesser Black-backed Gulls *L. fuscus*. The gulls' success rate could not be determined, but it seemed that the divers mostly escaped by either diving quickly or by a fast rush along the surface. It is possible that kleptoparasitism of divers is more common than my few observations and literature records suggest. Bergman (1960) observed Great Black-backed Gulls kleptoparasitise Black-throated Divers on several occasions and Goethe (1956) reports that wintering Red-throated Divers *G. stellata* were attacked by Herring Gulls and deprived of their fish, while King (1966) saw Herring Gulls unsuccessfully attack Great Northern Divers *G. immer*. Dittberner & Dittberner (1979) observed up to 12 Common Gulls that attended a small group of Black-throated Divers that was stopping over on a lake near Berlin. The gulls attempted to steal fish from the divers, mostly with poor success but the authors also recorded successful attacks on one of three observation days.

Great Crested Grebe Podiceps cristatus

In South Sweden, Great Crested Grebes occur in flocks or loose assemblages both during migration, especially on fish-rich lakes in late autumn, and as non-breeders in certain areas along the coast and on some lakes, e.g., Lake Vättern. Most of my observations of kleptoparasitism of Great Crested Grebes come from Lake Vombsjön in southern Skåne (c.55°40'N, 13°36'E), where sometimes more than 2000 Great Crested Grebes may be seen in November. Black-headed Gulls and, more often, Common Gulls associate with the flocks when the grebes are fishing actively. The gulls either circle and hover above the grebes, especially when fishing activity is high, or swim among them. Although kleptoparasitic attacks on the grebes by Common Gulls occur, this association may be predominantly commensal – apparently the gulls exploit fish that is forced towards the surface by the grebes' activity (Vinicombe 1976). Observation distances are often large at Lake Vombsjön, but the few kleptoparasitic attempts I have seen well, have nearly all resulted in the grebe diving quickly without losing its prey (only two attempts out of 20 resulting in the gull getting the fish). The same escape tactic was also used against Herring Gulls, which sometimes attended flocks of fishing Great Crested Grebes on Lake Vombsjön in low numbers. As for Common Gulls, Herring Gulls' success rate appeared to be very low because of the rapidity with which the grebes dived when attacked. I have, however, recorded a successful attack by a Herring Gull (Lake Vättern in April; five Herring Gulls attending a flock of 105 Great Crested Grebes and attacking grebes surfacing with fish). In addition to the grebes' fast diving when attacked, another factor may explain the kleptoparasites' low success rate, namely that grebes mostly capture fish that are small and quickly swallowed.

Instances of kleptoparasitism of Great Crested Grebes by Black-headed Gulls and Common Gulls have been reported in the literature, mainly in the form of short notes. Boyd (1944), Bergman (1960) and Lehmann (1978) all observed Black-headed Gulls associating with, and stealing fish from Great Crested Grebes that were feeding young. Jacoby et al. (1970) state that Black-headed Gulls associate with Great Crested Grebes on Lake Bodensee and kleptoparasitise them successfully, while Jacoby & Leuzinger (1972) in their analysis of the effects on the lake's wintering waterfowl assembly of the mass occurrence of the freshwater mussel *Dreissena polymorpha* say that Common Gulls earlier tended to associate with Great Crested Grebes but in later years turned to exploiting ducks and Eurasian Coots. Likewise in winter, Pettitt (1952), Sage (1963) and Neub (1970) saw a few attacks on Great Crested Grebes by Black-headed Gulls, and Dittberner & Dittberner (1979) by Common Gulls, while Berndt & Drenckhahn (1974) mention kleptoparasitism by Herring Gull, and rarely Great Black-backed Gull, of moulting Great Crested Grebes at Selenter See in Schleswig-Holstein.

Great Cormorant Phalacrocorax carbo

Fifty years ago the Cormorant was mainly a winter visitor to the Swedish west coast (with a single small newly established breeding colony in the Baltic). Since then the situation has changed completely and Cormorants (of southern origin) now breed over much of southern Sweden, at both inland and coastal sites. During autumn, large numbers can be seen flock-fishing not only in relatively large lakes such as Roxen (58°30'N, 15°38'E; H. Nilsson in litt.), but also in quite small ones such as Ellestadsjön (55°02'N, 13°02'; Andersson et al. 1991). During the last two decades several thousand birds have also been present during autumn at Falsterbo, roosting on a sandbar island and forming large fishing flocks on the surrounding sea. Huge numbers of Cormorants also fish in the sound between Sweden and Denmark in winter, the largest flock observed so far numbering c.13,000 birds (November 2005, K. Bengtsson pers.comm.) and in southern Kattegat, especially on the wide bay of Skälderviken.

Great Black-backed Gulls were sometimes seen to monitor solitarily fishing Cormorants and attack them when they had captured prey difficult to swallow. Also Herring Gulls sometimes attacked solitary Cormorants, but in this situation both gull species seemed to have rather poor success. One reason for this was that the Cormorant often threatened the gull, and tried to bite it. Once I even observed a Cormorant which, after having swallowed its fish, first directed vigorous pecks at a Great Black-backed Gull and then chased it in the air for several metres.

Mostly, however, it was the large fishing-flocks of Cormorants that were the target of the two large gull species. Depending on locality, flocks of fishing Cormorants also attracted Black-headed Gulls, Common Gulls (inland) and Kittiwakes *Rissa tridactyla* (at the coast). The former two species seemed to use the Cormorants mainly commensally, even though attacks by Common Gulls were seen occasionally. Kittiwakes, however, attempted to steal fish from them (Källander 2006). Flock-fishing Cormorants with associated large gulls were observed in all months, in spring, summer and sometimes also in autumn on lakes of different size; in autumn off the Falsterbo peninsula; and during winter on the bay of Skälderviken. Also at Lake Vombsjön flock-fishing took place in winter as long as the lake did not freeze (with Cormorant numbers sometimes exceeding 500).

Both at the coast and inland (Lake Vombsjön) observation distances were mostly large. Furthermore, in winter, fishing flocks of Cormorants often attracted a large number of gulls, among which intraspecific attacks, chases and other dominance interactions were common. This, together with the fact that many gulls often attacked the same Cormorant simultaneously resulting in a confusion of wings, made the recording of success rates difficult. At Lake Vombsjön about a fifth of recorded attacks were successful in both Great Black-backed Gull and Herring Gull (N = 32 and 49, respectively). However, Herring Gulls afterwards often lost the fish to a Great Black-backed Gull (see *Mergus* spp. below). As in other kleptoparasitic associations, both success and attack rates were strongly dependent on the size of prey caught by the Cormorants. This was well illustrated at Lake Vombsjön in late autumn 2005 when both Goosanders *Mergus merganser* and Cormorants fed on very small fish and the large gulls attempted very few attacks; none of those seen was successful. Later in winter both species were fishing in the deeper parts of the lake and brought up larger fish – and were intensively kleptoparasitised by the two large gull species.

Attempts at intra-specific kleptoparasitism were extremely common among flock-fishing Cormorants and a Cormorant that had captured a large fish that took some time to handle was nearly always attacked by conspecifics. A common escape tactic was to make a quick rush along the surface meanwhile trying to swallow the fish. This almost invariably released attacks from gulls, often from large distances. Also diving was used to escape from kleptoparasites. However, in contrast to some other hosts that immediately drop their prey when attacked by an interspecific kleptoparasite, Cormorants tried to resist attacks. Thus, on one occasion a Cormorant was seen to hold a firm grasp of its fish, with the gull and the Cormorant pulling in different directions, the Cormorant winning the struggle. Like solitary Cormorants, also flock-fishing Cormorants often bit and threatened gulls, and both Great Black-backed Gulls and Herring Gulls sometimes seemed hesitant to attack a Cormorant with fish.

There seem to be few literature reports on kleptoparasitism of Great Cormorants. Podmore (1973) describes how a Herring Gull snatched fish from a Cormorant near the Pembrokeshire coast, while Bruun (2001) presents a vivid series of colour photos of Great Black-backed Gulls kleptoparasitising Cormorants in a fishing harbour on the Swedish west coast. In the Aegean, Yellow-legged Gulls *Larus cachinnans/michahellis* hovered over flock-fish-

ing Common Shags *Phalacrocorax aristotelis* and robbed them of fish, mostly successfully (Jönsson 1984). Likewise, K.-B. Strann (in litt.) reports a much higher success rate for Great Black-backed Gulls when parasitising Shags than when parasitising Cormorants in North Norway. Also Duchrow (1958) noted that Shags often dropped their prey when attacked by Audouin's Gulls *Larus audouinii*.

Whooper Swan Cygnus cygnus

Herring Gulls' kleptoparasitism of Whooper Swans feeding on sand-gapers *Mya arenaria* in the shallow waters of the Sound was described by Källander (1975), who also depicted the often very fierce attacks on the swans, which included the gull vigorously biting the swan's neck. Forty-seven per cent of 504 attacks resulted in the gull obtaining food. This kind of kleptoparasitic association has also been observed in other places along the Swedish west coast in winter (Getterön, C. Johansson in litt.; Skälderviken, pers.obs.) but may have become less common in later years as Whooper Swans have increasingly turned to grazing inland.

Tufted Duck Aythya fuligula *and*
Greater Scaup A. marila

The Tufted Duck breeds all over Sweden (Svensson et al. 1999) and is also a common winter visitor around the southern coasts, not least around the southernmost province, Skåne (Nilsson 1991, 2005). The Scaup has a similar winter distribution to the Tufted Duck, with which it usually associates, but is much less common. Observations of gull kleptoparasitism therefore almost exclusively refer to the Tufted Duck. In winter this species is largely a nocturnal feeder but the proportion of individuals diving during daytime is negatively related to temperature (Nilsson 1970) and particularly in severe winter conditions Tufted Ducks may dive intensively also during the day. Consequently, almost all observations were made in January and February, most of them during cold winters. At the coast, Tufted Ducks fed on bivalves, probably almost always blue mussels *Mytilus edulis*.

Although I recorded a few kleptoparasitic attacks by Black-headed Gulls on Tufted Ducks, including positive ones, and one by a Great Black-backed Gull, it was only Herring Gulls that regularly used Tufted Ducks as hosts. The gulls swam among the ducks in an alert posture and, when a duck surfaced with a mussel, immediately flew towards it from distances of up to 15 metres. The duck would then dive with the gull plunging headlong after it. Probably the duck often dropped its prey as it dived, because in 52% of the cases (N = 34) the gull obtained the food item. During one 10-min observation bout, 22 positive attacks by 18 Herring Gulls were recorded, corresponding to 0.28 stolen food item/gull/min. The three observed attacks on Scaup were in all respects similar to those on Tufted Ducks (but were all positive from the gull's point of view).

Herring Gulls attending Tufted Ducks tended to keep small "territories" or a certain distance to

Juvenile Herring gull attending Goosanders.
Ung gråtrut som bevakar fiskande storskrakar i Ystad hamn, 1 mars 1964.

Black-headed Gull pursuing Lapwing with eartworm in flight.
Skrattmås som i luften förföljer tofsvipa med mask, Revinge oktober 1973.

other gulls. On several occasions the gull-to-duck ratio was as low as 1:100, on others the ratio was considerably higher (e.g., 1:10). Very low ratios may be explained by the fact that only some of the Tufted Ducks in a flock were diving at a particular time and so could be exploited by the gulls.

Kleptoparasitism of Tufted Duck and Scaup by gulls in winter may be both more common and more widespread than reports in the literature suggest. Occasional kleptoparasitic attacks on Tufted Ducks by Black-headed Gulls on park ponds, water reservoirs and similar inland waters have been reported by Massingham (1921), Pettitt (1952), Meinertzhagen (1959), Harrison & Harrison (1962), Stichmann (1962) and Sage (1955, 1963), while attacks by Common Gulls have been reported by Schmidt (1954), Bezzel (1958) and Jacoby & Leuzinger (1972), but in the latter three cases hosts other than Tufted Duck were much more important. de Leeuw & Renema (1997) found that during daytime diving Tufted Ducks lost 60% of their *Dreissena* mussels to Black-headed Gulls, Common Gulls and Eurasian Coots. These authors speculated that feeding at night might be an adaptation to avoid food loss to kleptoparasites. According to Steiniger (1952) and Schmidt (1954) wintering Scaup along the German coast were regularly parasitised by Herring Gulls and Common Gulls.

Common Eider Somateria mollissima

Beside the association of Black-headed Gulls and Common Gulls with Lapwings and Golden Plovers, that of Herring Gulls, and sometimes Great Black-backed Gulls, with Eiders is probably the most common and widespread one in South Sweden and occurs in all months of the year. It is, however, most commonly seen during those parts of the year when Eiders occur in flocks, in particular in winter and during spring migration. Large flocks of diving Eiders may be attended by considerable numbers of Herring Gulls. Thus, the huge flocks of Eiders wintering off the Dutch coast, which may number several tens of thousands of birds, can have several thousands of large gulls hovering above them (pers. obs.).

Common Eiders feed mostly on blue mussels, sometimes quite large (Madsen 1954) and therefore potentially suitable prey for Great Black-backed Gulls. Nonetheless, in my material Eiders were attended by Herring Gulls more than ten times as often as by Great Black-backed Gulls (data from 51 different dates). Even though Herring Gulls are normally more numerous than Great Black-backed Gulls, this cannot explain this observation, because also in areas where Great Black-backed Gulls were common, it was quite rare to see them associated with Eiders; but see Schmidt (1954). So, apparently Great Black-backed Gulls did not normally regard it profitable to kleptoparasitise Eiders. Although mussels were their normal prey, Eiders were also seen to be robbed of fish and, in harbours, of fish offal.

Kleptoparasitising gulls usually swam among the Eiders and attacked when an Eider surfaced with food, but sometimes they would circle and hover above a flock. Like other diving ducks Eiders tried to escape from attacking gulls by diving but when doing so often dropped their prey. Herring Gulls had an overall success rate of 38.5% when

parasitising Eiders in winter (N=325 recorded attempts), with no statistically significant difference between three recognised age classes of gull (first winter birds, immatures and adults) (χ^2=1.86, df 2, P=0.40).

Kleptoparasitic interactions between gulls and Eiders have received some attention in the litterature and is already mentioned in a Danish manuscript from 1767 (Helms 1936). Both Ingolfsson (1969) and Prys-Jones (1973) described how Glaucous Gulls *Larus hyperboreus* defended Eider rafts against other gulls. The first author also presented data on the proportions of gulls of five species that engaged in kleptoparasitism of Eiders at an Icelandic locality. He showed that Glaucous Gulls and Herring Gulls were the species that associated with Eiders the most; Great Black-backed Gulls did so to a very small extent and Lesser Black-backed Gulls and Iceland Gulls *Larus glaucoides* not at all. While parasitism of Eiders by Great Black-backed Gulls has been mentioned by, e.g., Roberts (1934) and Schmidt (1954), Herring Gulls figure more often in this situation (Steiniger 1952, Duchrow 1958, Bergman 1960, Sage 1963), in agreement with my own data from South Swedish coasts. Interestingly, when a flock of Eiders stayed the 1970/71 winter on Lake Bodensee, where they fed on *Dreissena* mussels, they were regularly kleptoparasitised by Herring Gulls (Jacoby & Leuzinger 1972).

Scoters Melanitta *spp.*

The material contains only two records of gulls associating with scoters: several Herring Gulls attacking Velvet Scoters *M. fusca* near the coast in southern Kattegat in late June and two Herring Gulls attending a flock of Black Scoters *M. nigra* on the bay of Skälderviken in winter. The scarcity of observations probably reflects both that scoters are relatively few in areas close to the coast (Nilsson 2005) and also my own excursion pattern. I have seen Herring Gulls kleptoparasitise Black Scoters near the coast of North Wales in winter and considering that both species feed on bivalves (Bauer & Glutz 1969) it would be surprising if they were not regularly parasitised by Herring Gulls in their winter quarters. In agreement with this, Schmidt (1954) mentions both Common Gulls and, more regularly, Herring Gulls as kleptoparasites of Black Scoters; also Sage (1963) reports an observation of Herring Gulls parasitising a flock of Black Scoters. Schenkeveld & Ydenberg (1985) often observed Glaucous-winged Gulls *Larus glaucescens* stealing mussels from Surf Scoters *Melanitta perspicillata* and presented evidence that synchronous diving is an adaptation that reduces their loss of food to kleptoparasitic gulls.

Common Goldeneye Bucephala clangula

Flocks of Goldeneye were regularly attended by Herring Gulls in winter (December to early March), with most observations in February. The gulls swam among the Goldeneyes and attacked birds that surfaced with prey but did so with very low success (10%, N=87). Three of the positive attacks were on goldeneys with fish and if these are excluded, overall success rate drops to 7%. This low success rate no doubt was a consequence of the prey taken by Goldeneyes normally being very small along the coasts where my observations were made. North of Gothenburg, where Goldeneyes were taking shore crabs *Carcinus moenas*, eight out of 14 attacks by Herring Gulls were successful (H. Dow in litt.). Another indication that Goldeneys normally took very small prey is the fact that on numerous occasions Herring Gulls were seen closely attending diving flocks of Goldeneyes without making any attacks. When attacked, Goldeneyes avoided losing their prey by diving quickly, but twice Goldeneyes were seen being chased in the air by a Herring Gull. In one of these the prey was a fish; in the other, the prey could not be identified. In the latter case the Goldeneye landed with its prey and dived immediately.

Literature reports of gull parasitism of Goldeneye seem to be few and restricted to casual observations (Pearse 1921, Glegg 1944, Bergman 1960, Stichmann 1965, Neub 1970, Grace 1980). The reason for this scarcity probably is that Goldeneyes normally feed on very small prey (Bauer & Glutz 1969), as also stressed by Jacoby & Leuzinger (1972). It may be significant that four of the above references report cases where Goldeneye had captured fish. Seen in this light, it is rather surprising that Herring Gulls were so frequently seen attending Goldeneyes along the Swedish south coast in winter.

Goosander Mergus merganser*, Red-breasted Merganser* M. serrator*, Smew* M. albellus

One of the most widespread kleptoparasitic associations in South Sweden and elsewhere is that between the large gull species on the one hand and Goosander and Red-breasted Merganser on the other. In late autumn, Goosanders gather in large numbers on some South Swedish lakes, such

as Lakes Mälaren, Hjälmaren, Roxen and Åsnen. From the latter two lakes there are reports of up to 25,000 (Druid & Tranesjö 1995) and 13,000 birds (O. Bondesson in litt.). The Goosanders form dense fishing flocks often numbering several thousand individuals, and these regularly attract numerous gulls, mainly but not exclusively Herring Gulls at these inland sites.

Also the more marine Red-breasted Mergansers assemble in autumn in large flocks in at least one area of South Sweden, namely immediately to the south of the Falsterbo peninsula, where peak numbers of 4000 have been recorded in late September and early October (Roos 1982). Like the Goosanders, the Red-breasted Mergansers off Falsterbo form large, dense feeding aggregations of sometimes thousands of birds (not seldom mixed with Cormorants). These flocks attract hundreds of large gulls but as the mergansers fish far out at sea no details can be seen from land. However, also small groups of Goosanders and Red-breasted Mergansers tend to be attended by gulls, Goosanders sometimes in winter even on relatively small streams.

Although most Goosanders and Red-breasted Mergansers winter in areas further to the southwest, both species are relatively common along the South Swedish coasts in winter (Nilsson 1991, 2005), with Goosanders in harbours and close to the shore and Red-breasted Mergansers further out on the open sea. Ninety-five percent of my observations of parasitism of Goosanders by Great Black-backed Gulls and Herring Gulls refer to the winter period (November to March), reflecting the Goosander's distribution during that season. For the Red-breasted Merganser, observations were more evenly spread over the year but with a peak in October (Falsterbo) and one in January–February.

Also Common Gulls, and sometimes Black-headed Gulls *L. ridibundus*, associated with flock-fishing Goosanders and Red-breasted Mergansers. Although both species have been seen to attack mergansers with fish, this association may be predominantly commensal. However, Common Gulls at Lake Vombsjön also regularly attacked flock-fishing Goosanders even though their success rate was low (two out of 18 recorded attacks).

The two main kleptoparasites of Goosanders and Red-breasted Mergansers, the Great Black-backed Gull and the Herring Gull, seem to differ in the frequency with which they associate with the two host species. However, a proper analysis of this requires that all four species occur together in the same area. This is the case along the south coast of Skåne in winter; there, Great Black-backed Gulls showed a strong tendency to attend Goosanders and, conversely, Herring Gulls to be associated with Red-breasted Mergansers ($\chi^2_{(1)}$=36.2, P<0.001, N=172 cases). Great Black-backed Gulls were thus found with Goosanders seven times as often as with Red-breasted Mergansers, while Herring Gulls were associated with Red-breasted Mergansers more often than with Goosanders.

Both species of large gull had a higher success rate when parasitising Goosanders than Red-breasted Mergansers (Fisher Exact test, Great Black-backed Gull, P=0.03; Herring Gull, P=0.05), with the Great Black-backed Gull having a higher success rate (53%, N=102 attacks) than the Herring Gull (28%, N=158 attacks) when parasitising Goosanders ($\chi^2_{(1)}$ =16.62, P<0.001). When parasitising Red-breasted Mergansers there was no difference between the species but number of recorded attacks by Great Black-backed Gulls was low. Both attack rate and success rate varied with the size of prey taken by the host.

Similar to Cormorants, both Goosanders and Red-breasted Mergansers tried to escape from kleptoparasites by rushing along the surface or by diving. Especially Red-breasted Mergansers often dived quickly when attacked. Observations suggested that the chosen escape method was related to the size of prey, with surface rushes being more common when the fish was large. Intraspecific kleptoparasitism was very common, at least in Goosanders and, as in Cormorants, triggered kleptoparasitic attacks by Herring Gulls and Great Black-backed Gulls, at the coast sometimes from distances of up to c.100 metres.

At the coast, kleptoparasitism of Goosanders was very much a phenomenon of severe winter conditions when Goosanders became concentrated in ice-free areas, such as certain harbours. As an example, in February 1985 Goosanders were fishing in the harbour of Ystad on the south coast, where big ferry boats prevented the harbour from freezing over. The fish they captured were often quite big (flatfishes Pleuronectidae and probably cod *Gadus morrhua* and ide *Leuciscus idus*). Their capture rate of fish appeared to be very high, as indicated by the fact that feeding bouts were interrupted by periods of resting and preening. Nevertheless, intraspecific kleptoparasitism was extremely fierce and a Goosander that had captured a large fish was often chased over long distances by several others, who even climbed the back of the fleeing bird in attempts at stealing the fish. These chases elicited attacks from the many large gulls that were either swimming among the Goosanders or standing on

the ice. Although Great Black-backed Gulls made up only 20% of the large gulls they obtained 88% of the fish stolen from Goosanders ($\chi^2_{(1)}$=30.4, P<0.001). Because of their physical dominance they often supplanted Herring Gulls that had initiated attacks on Goosanders but they also forced Herring Gulls to drop stolen fish. Thus, 16 times that a Herring Gull had obtained a fish, it lost it to a Great Black-backed Gull 11 times, whereas in no case was a Herring Gull seen to steal a fish from a Great Black-backed Gull.

Kleptoparasitic attacks on Smews were also observed a few times in winter. For instance, in an embankment in Malmö Herring Gulls were once seen repeatedly, but unsuccessfully, attacking fishing Smews, the latter immediately diving when attacked.

Gull kleptoparasitism of Red-breasted Mergansers has been mentioned in a few papers. Kumerloeve (1953) reports that both Black-headed Gulls and Common Gulls snatched fish from surfacing Red-breasted Mergansers, while Nilsson (1965) saw both Herring Gulls and Lesser Black-backed Gulls attend fishing groups of Red-breasted Mergansers in southeastern Sweden in spring. Although he observed several attacks on the mergansers, which normally tried to escape by rushing along the water surface, none was successful. Kleptoparasitism of Goosanders (and the conspecific American Merganser) has been reported more frequently. Lovell (1945) states that eight American Mergansers that were parasitised by some 12–15 Herring Gulls on a winter day lost most of their captured fish to the gulls. Schmidt (1958) gives a very vivid description of parasitism of wintering Goosanders by Great Black-backed Gulls in particular, while Bengtson (1966), Nilsson (1966), Ritzel (1978), Sellin 1986) and Berndt & Busche (1993) report observations of kleptoparasitism by the two large gull species, also in winter.

From the Continent, there are reports of both Black-headed Gulls and Common Gulls parasitising Goosanders in winter. While those of Bezzel (1958) and Neub (1970) refer to single observations, Steinbacher (1929) and Stichmann (1965) say that this is a regular phenomenon in Common Gulls and Black-headed Gulls, respectively, and the latter author also describes the gull's behaviour in some detail.

Individual Ring-billed Gulls *Larus delawarensis* that during a period in winter stole fish from a group of American Mergansers tended to monopolise the group (Lamore 1953), a behaviour often seen in both Great Black-backed Gulls and Herring Gulls and which is successful at small flocks of mergansers but not at large fishing-flocks (pers. obs.). Bergman (1960), finally, observed Herring Gull kleptoparasitism of Goosanders in summer and also referred to observations of Goosander broods being parasitised by Common Gulls.

Eurasian Coot Fulica atra

Although Coots often feed on mussels in winter, I made few observations of gulls kleptoparasitising them. Eight of these were during December–February, one in April. One involved a Common Gull, another a Black-headed Gull and in both cases the interaction appeared to be rather casual; in the remaining seven cases, Coots were parasitised by Herring Gulls. The Herring Gulls swam among the Coots and attacked as these brought mussels to the surface. The Coots tried to avoid losing their prey by a fast rush, but the limited data indicate that the gulls were quite successful (11 out of 15 recorded attacks). These data originate from southern Kattegat, where blue mussels in shallow waters attain a larger size than in the Sound and the Baltic, where most of the wintering Coots are found (Nilsson 2005).

Kleptoparasitism of Coot seems to be quite common on the Continent in winter, where either Common Gulls or Black-headed Gulls, or both, are the parasites. Apart from a few rather casual observations (Pettitt 1952, Harrison and Harrison 1962, Wagner 1962, Stichmann 1965, Neub 1970, Strunk 1975), some of which refer to the stealing of fish, Bezzel (1958), Géroudet (1966), Jacoby & Leuzinger (1972) and Baccetti (1987) characterise the association between Coots and the two small gull species as a regular phenomenon. The studies by Géroudet and by Jacoby and Leuzinger refer to Lake Geneva and Lake Bodensee, respectively, where large numbers of Coot feed in winter on the rich beds of *Dreissena* mussels. Jacoby & Leuzinger (1972) report a maximum count of 72,000 Coot on Lake Bodensee and speculate that the increase in the number of wintering Common Gulls there is a result of their obtaining *Dreissena* mussels through kleptoparasitism (of Coots in particular). Also American Coots are parasitised by gulls (Bartlett 1957, Rüppel 1977, Grace 1980), in the cited cases by Ring-billed Gulls; Rüppel presents photographs of the Coots' escape method (p. 168).

Eurasian Oystercatcher Haematopus ostralegus

Only twice have I seen gulls kleptoparasitise Oystercatchers in Sweden, once each in July and Au-

gust. On both occasions the Oystercatchers were feeding on earthworms in ploughed fields. On the first, only three Oystercatchers were present, but Common Gulls attacked them when they had extracted a worm. When attacked, the Oystercatchers responded by running away and swallowing the prey. They then turned around and threatened the gull. Apparently some attacks were nonetheless successful. On the second occasion nine Oystercatchers were spread out over a field and both Black-headed Gulls and Herring Gulls were seen attacking them, the former making three quick and successful attacks when an Oystercatcher had just extracted a worm and was about to pick it up. In these cases the Oystercatchers were remarkably indifferent but twice when an Oystercatcher had already swallowed the worm when the gull arrived, it threatened the gull and even ran after it. Also the Herring Gulls were seen to make successful attacks a couple of times, the Oystercatcher running away at the approach of the gull, leaving the worm on the ground. However, during an aerial chase the Herring Gull was easily outflown by the Oystercatcher.

I have seen Black-headed Gulls steal earthworms from Oystercatchers in North Wales in mid-winter and find it a bit surprising that I have come across only one literature report on this kind of parasitism (Mills 1980) considering that, in certain conditions, Oystercatchers relatively often search for earthworms in grassland. In contrast, there are several descriptions of both Common Gulls and Black-headed Gulls kleptoparasitising Oystercatchers on mudflats, where they steal either ragworms *Nereis*, or various kinds of bivalve (e.g. Etienne and Triplet 1986, Sueur 1993, Triplet 1993). The stealing of bivalves from Oystercatchers by different species of gull has been analysed by Ens & Cayford (1996), who also provide several references. Also on tidal shores in other parts of the world other species of oystercatcher are parasitised by gulls, African Black Oystercatcher *Haematopus moquini* by Kelp Gulls *Larus dominicanus* (Hockey 1980), American Oystercatcher *Haematopus palliatus* by Brown-hooded Gulls *Larus maculipennis*, Grey-hooded Gulls *L. cirrocephalus* and Band-tailed Gulls *L. belcheri* (Martinez & Bachmann 1997, Khatchikian et al. 2002).

Tinbergen & Norton-Griffiths (1964) described how Oystercatchers breeding in a colony of Black-headed Gulls were robbed by the gulls when they returned with mussels to feed their young. Especially juvenile gulls engaged in the kleptoparasitism. The Oystercatchers tried to escape by running and were not aggressive towards juvenile gulls, but often threatened the adults. Also the Oystercatcher chicks lost food to the gulls.

Golden Plover Pluvialis apricaria *and Northern Lapwing* Vanellus vanellus

The kleptoparasitic association of Black-headed Gulls and Common Gulls with Golden Plovers and, in particular, Lapwings was the one most frequently seen. Black-headed Gulls' behaviour when stealing earthworms from Lapwings was described by Källander (1977), who also presented a diagram of the seasonal occurrence of this kleptoparasitic association in South Sweden (Källander 1979). The behaviour showed a brief peak in spring when Lapwings occur in flocks (sometimes absent in warm springs) and a more extended occurrence during autumn, peaking in late September–October. Kleptoparasitism of Golden Plovers in South Sweden showed a similar pattern, with a peak in October, but in spring seemed to occur only during periods of cold weather when flocks of Golden Plovers stopped-over (mainly in grassland).

Black-headed Gulls' kleptoparasitism of both Lapwings and Golden Plovers has been analysed in great detail by Barnard & Thompson (1985), while Källander (2000) showed how juvenile gulls' success rate increased from July to November. Here only some comparisons will be made of the success rates of Black-headed Gulls and Common Gulls when parasitising the two plover species.

Overall success rate when parasitising Lapwings (a mean figure for adults and juveniles calculated over the whole year) was 55.5% (N=12 453 attacks) for Black-headed Gulls and 55.6% (N=1831 attacks) for Common Gulls, i.e. identical for the two species. However, when parasitising Golden Plovers, Common Gulls had a higher success rate than Black-headed Gulls (52.0% vs 42.0%, $\chi^2_{(1)}=10.06$, P=0.002, N=577 and 443 attacks, respectively). This was probably due to the Common Gull's faster flight and perhaps also to its larger size and therefore more scaring appearance. Adults of both species had higher success rates than juveniles when parasitising Lapwings (P<0.001 in both cases). Also when parasitising Golden Plovers adult Common Gulls were more proficient than juveniles ($\chi^2_{(1)}=4.36$, P=0.04), but no corresponding difference was found for Black-headed Gulls, probably because of a rather limited sample size.

I also made five observations of Herring Gulls kleptoparasitising Lapwings. One of them was casual and like another two cases probably involved

only a single gull. However, in the morning of 20 August 1970 a number of Herring Gulls, together with Common Gulls and Black-headed Gulls, were spread out in a flock of Lapwings feeding in a bare field on the island of Gotland in the Baltic. The Herring Gulls attacked Lapwings that had found an earthworm in much the same way as the smaller gull species do and several successful attacks were seen. Most of these were when the Lapwing dropped the worm quickly and fled; in most aerial chases the Herring Gull gave up already after a few metres, but a few long chases, including a successful one, were also seen. Kleptoparasitism of Lapwings by Herring Gulls has been mentioned in the literature (Johnston 1945).

Curlew Numenius arquata

All but one observation of kleptoparasitism of Curlews were made in late March–early April when migrating Curlews were stopping over in grassland. In two cases Common Gulls closely attended a flock of Curlews and made a few unsuccessful kleptoparasitic attempts. In the others, flocks of Curlews were feeding in grassland during cold spring weather and were parasitised by varying numbers of Black-headed Gulls. The gulls attacked the Curlews when these extracted an earthworm, sometimes already when the Curlew's movements indicated that it had found a worm. The Curlews used three different methods to avoid losing prey: (1) by crouching and pointing the bill towards the gull, a threat that usually made the gull inhibit its attack; (2) by running away in zig-zag; and (3) by taking flight. The gulls' success rate was c.15% (N=155 attacks), with both ground attacks and aerial chases sometimes resulting in the gull obtaining the worm. However, the profitability of parasitising Curlews seemed to be low. Thus, during 120 "gull minutes" on average a gull obtained less than 0.1 earthworm/min or about a third of what Black-headed Gulls can obtain by kleptoparasitising Lapwings (Källander 1977). In agreement with this, once when both Lapwings and and a flock of Curlews were feeding in a field, all gulls were associated with the Lapwings and none with the Curlews.

In South Sweden gull kleptoparasitism of Curlews is probably restricted to cold periods during the spring migration period which make Curlews stop over and feed in grassland. In such a situation, Arnell (1981) observed kleptoparasitism by Common Gulls of a large Curlew flock in South Central Sweden in early May. However, in the Curlews' wintering areas in western Europe, where large flocks may be seen foraging in fields, this form of kleptoparasitism is probably more common even though this does not seem to be reflected in the literature. Thus, I have seen kleptoparasitism inland in winter in both North Wales and the Netherlands. Kleptoparasitism of Curlews on mudflats has, however, been mentioned by Ens et al. (1990) and Sueur (1993).

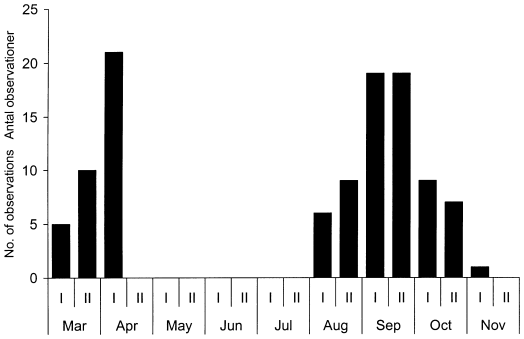

Figure 1. Number of days in each half-month period on which Black-headed Gulls or Common Gulls were seen kleptoparasitising Common Starlings. Most spring observations refer to parasitism of flocks of Starlings stopping over on migration, while most autumn observations were made in connection with farming operations.
Antal dagar i varje halvmånadsperiod som skratt- eller fiskmåsar sågs kleptoparasitera starar. De flesta vårobservationerna gjordes då starar rastade under vårsträcket medan flertalet höstobservationer gjordes i anslutning till jordbruksaktivitet.

Other waders

A few times Black-headed Gulls were seen stealing earthworms from Wood Sandpiper *Tringa glareola* and Ruff *Philomachus pugnax* on flooded meadows, but this kleptoparasitism was purely opportunistic in the sense that the gulls were not monitoring the feeding activities of the waders in the way they do when parasitising Lapwings or Golden Plovers but were feeding on their own and attacked only when a bird close to them had found a worm. Stealing attempts directed at Ruffs had low success, the Ruff running quickly in zig-zag; those directed at Wood Sandpipers were few but were more successful because the sandpiper immediately dropped its prey.

Calvario et al. (1984) saw seven adult Black-headed Gulls successfully stealing earthworms from Ruffs on a flooded meadow north of Rome in March, and Payne & Howe (1976) described a situation in which Dunlin *Calidris alpina* and Grey

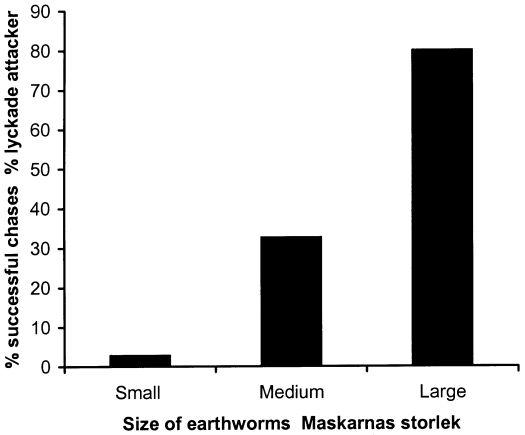

Figure 2. The proportion (%) of successful kleptoparasitic attacks by Black-headed Gulls on Common Starlings in relation to the size of the Starling's earthworm prey. Data were collected on a cold day in April when a large flock of Starlings was feeding in a field of winter wheat. N = 111 attacks.
Andelen attacker av skrattmås mot starar, där måsen lyckades stjäla starens daggmask, i relation till maskens storlek. Data från en kall dag i april, då en stor starflock födosökte på en åker med höstvete. N = 111 attacker.

Plover *Pluvialis squatarola* were feeding on earthworms in a recently flooded ploghed field and were parasitised by Ring-billed Gulls and Bonaparte's Gulls *Larus philadelphia*. In this case, the gulls were not foraging on their own but were monitoring the feeding activities of the waders, attacking them, mostly successfully, when they had found an earthworm. I have seen Black-headed Gulls rob Black-tailed Godwits *Limosa limosa* of earthworms on flooded grass in northwestern England in winter, the gulls' success rate being at least as high as when parasitising Lapwings. Black-headed Gulls also had a high success rate (57%) when stealing red swamp crayfish *Procambarus clarkii* from Black-tailed Godwits (Amat & Aguilera 1990).

On mudflats, gulls may parasitise different species of wader. Sueur (1993) analysed the factors determining the gulls' choice of host and found the proportion of annelids, especially *Nereis diversicolor*, to be the most important one. Gulls had a 50% success rate when parasitising Bar-tailed Godwits *Limosa lapponica* versus 18% when parasitising Redshanks *Tringa totanus*. Also Vader (1979) reported high success rates (25–75%) for Common Gulls robbing Bar-tailed Godwits of lugworms *Arenicola marina*.

Fieldfare Turdus pilaris *and Redwing* T. iliacus

Parasitism of Fieldfares (and occasionally of Redwings) by Black-headed Gulls was recorded on only 13 days, all but one in April, and was associated with cold weather making Fieldfares stop over in great numbers on grass. This cn be compared with observations of gull-Lapwing kleptoparasitism on more than 100 days and of gull-Starling parasitism on more than 40 days, during the same period in spring. The gulls would either circle over foraging Fieldfares and dive towards birds that had extracted an earthworm or stand alert in the flock waiting for a thrush finding a worm. Both methods sometimes resulted in a positive attack, but Fieldfares behaved very nervously when gulls circled above them and often took to the wing when a gull flew low over them. Kleptoparasitic attempts resulted in aerial chases of varying length. Positive attacks were recorded on both Fieldfares and Redwings, but despite the fact that earthworms were often very large, the gulls' energy gain seemed to be low. Thus, during 30 minutes ten black-headed gulls made only 15 positive attacks, or 0.05/gull/min.

Kleptoparasitism of thrushes has been mentioned occasionally in the literature (Anon. 1952, Vernon 1972, Burgess 1974). The last author saw Black-headed Gulls scattered among Fieldfares on short grass attempting to steal earthworms from them; their success rate was, however, relatively low.

Corvids Corvus *spp.*

Opportunistic attacks by Common Gulls on Western Jackdaws *Corvus monedula* and Rooks *C. frugilegus* that had found an earthworm were sometimes seen, in particular in connection with ploughing operations. Normally I paid these little attention, but none of eight recorded attacks on Jackdaws and 15 on Rooks was successful. I have found no references to this kind of kleptoparasitism, possibly because most observers have regarded it rather uninteresting. Andersson (1971) described how Common Gulls wintering in Lund, South Sweden, apparently to a great extent subsisted on stealing bread from Jackdaws. The gulls circled over the buildings and attacked Jackdaws that had brought a piece of bread to a roof or chimney to dismember it. No doubt this behaviour is widespread in those towns and cities in South Sweden where Common Gulls winter.

Common Starling Sturnus vulgaris

Starlings were subjected to kleptoparasitism by Common Gulls and Black-headed Gulls mainly in two very different situations. One was during cold spells in early spring when Starlings formed dense feeding flocks. About 75% of spring observations were of this kind and about 60% of these were on grass. The other situation was in autumn on agricultural land, mostly in connection with farming operations, especially ploughing (Figure 1). Of the autumn observations, more than half were of the latter kind, with another 40% in fields that had already been ploughed or harrowed (when Starlings mostly fed there together with Lapwings and sometimes also Golden Plovers).

In the first situation, i.e. when gulls parasitised dense flocks of Starlings in spring, they used two different methods to steal earthworms. Either they stood or walked in an alert posture within the flock of Starlings and, when a Starling extracted a worm, either ran or flew quickly towards it. The Starling tried to avoid the attack by running or flying a short distance, in both cases making sharp turns. Sometimes such attacks resulted in an aerial chase of varying length. The other method that gulls used was to circle low above the Starling flock and attack from the air, the Starling's escape behaviour being the same.

In autumn, gull kleptoparasitism of Starlings appeared to have a more opportunistic character. During ploughing operations, when the plough had passed, gulls settled waiting for the plough to return. By contrast, Starlings, when present, continued finding earthworms in the furrows and were then attacked by the gulls. However, also in other situations when gulls and Starlings were feeding in the same fields, gulls tried to steal earthworms from them.

As in other kleptoparasitic associations, the parasite's success rate was dependent on the size of the prey and consequently on the host's handling time. Figure 2 illustrates this with data collected on a cold day in April when Black-headed Gulls were engaged in an intense kleptoparasitism of a large flock of Starlings on young winter wheat.

Overall a third of all recorded attacks over the years (N=950 for the two gull species combined) were successful, but this figure tells us rather little, because the efficiency of the two types of attack differed greatly. Thus 38.4% of long aerial chases by Black-headed Gulls were successful and 44.1% of those of Common Gulls vs only 15.8% and 18.7%, respectively, of attacks on foot or after a short aerial chase, two highly significant differences (Black-headed Gull: $\chi^2_{(1)}=11.43$, P=0.001, N=152); Common Gull: $\chi^2_{(1)}=14.95$, P<0.001, N=263). Long aerial chases often lasted half a minute, sometimes more, when the Starling tried to escape its follower by rising in the air or making quick turns when the gull caught up. When Starlings managed to keep their worm after a long chase they showed a pronounced tendency to return to the flock to consume it. This meant that they were often intercepted by the gull and the chase continued. On a few occasions in spring Starlings that had found a worm flew into tall grass to eat it undisturbed, and in one instance Starlings escaped a few times from chasing Black-headed Gulls by perching in shrub.

On a cold day in late March a single Herring Gull that had associated with Common Gulls, Black-headed Gulls, Lapwings and Starlings was seen to make two unsuccessful attempts to steal earthworms from Starlings.

Despite that kleptoparasitism of Starlings appears to be relatively common, I have found no literature records of this behaviour in a natural situation. Neither do Brockmann & Barnard (1979) in their review of kleptoparasitism in birds mention Starlings as hosts of Common Gulls or Black-headed Gulls. However, at a refuse dump in New Jersey, Burger & Gochfeld (1979) studied age differences in the kleptoparasitism of Starlings by Ring-billed Gulls.

Discussion

Types of interspecific kleptoparasitism

In the above account I have used the terms 'opportunistic' and 'regular' to characterise interspecific kleptoparasitic interactions. Opportunistic stealing of food occurs when different species forage in close proximity for reasons other than making kleptoparasitism possible. Often this means that two or more species are attracted to the same rich source of food, for instance earthworms made available behind a plough. In such situations, the presence of a prey item in the bill of another individual may trigger an attempt at stealing it. Although this kind of food stealing may increase the kleptoparasite's energy gain, it is less interesting than regular kleptoparasitism in which the kleptoparasite recognises, and associates with particular host species, at least when the latter are actively foraging. Examples are Common Gulls and Black-headed Gulls associating with Lapwings and Golden Plovers, Herring Gulls with Eiders and Great Black-backed Gulls and Herring Gulls with Cormorants and mergan-

sers. In these cases the kleptoparasite apparently has learnt to associate the host species or its feeding activity with potential food.

Another feature that characterises regular kleptoparasitism is that, in contrast to opportunistic food stealing, the kleptoparasite does not normally search for any food itself but relies on the host's food finding ability. One could argue that the two types of kleptoparasitism only represent the endpoints of a continuum rather than a clear dichotomy. For instance, situations exist when a kleptoparasite combines self-feeding and food stealing (e.g., Ens et al. 1990), but field studies have shown that this is normally not the case (e.g. Payne & Howe 1976, Källander 1977, Buckley 1987) and has also been shown theoretically not to be an optimal strategy (Broom & Ruxton 1998). Opportunistic and regular kleptoparasitism therefore seem to be useful terms for describing kleptoparasitic interactions.

In what situations does interspecific kleptoparasitism occur?

Disregarding other benefits and costs, one would expect interspecific kleptoparasitism to occur whenever the kleptoparasite's net intake rate through kleptoparasitism is greater than by its use of other feeding methods. Obvious examples are when hosts (e.g. Cormorants, diving ducks) make food available that would otherwise be out of reach for the kleptoparasite or when hosts (Lapwings, Golden Plovers, Oystercatchers) are much more efficient than the parasite at detecting hidden prey. In addition, kleptoparasitism should be expected to occur in situations of absolute or relative food scarcity (Furness 1987), a notion that is supported by the observation that several of the associations described in this paper occurred in harsh winter conditions or during cold spells in spring (for other examples of temporary food scarcity increasing the incidence of kleptoparasitism, see Oro & Martínez-Vilalta 1994, Oro 1996, Beintema 1997).

Because of inferior competitive ability and poorer food finding ability (e.g. Greig et al. 1983), food scarcity may strike juveniles harder than adults. Kleptoparasitism should therefore be a more common feeding method in young birds, as also found in some studies (Verbeek 1977, Rockwell 1982, Steele & Hockey 1995). At a site where both adult and juvenile Black-headed Gulls kleptoparasitised different hosts, Amat & Aguilera (1990) found that juveniles attacked less profitable hosts more often than adults did, probably an effect of competition between the age classes. In many situations, however, competition between the age classes of Black-headed Gulls seems to be reduced by differential daytime distribution (Källander & Rosenkvist 2000), rather than by use of different foraging methods, and so far I have found no difference in the frequency with which the two age classes kleptoparasitise Lapwings in South Sweden.

Factors affecting the kleptoparasite's success rate

Apart from factors such as the host's ability to defend its food or to evade an attack, a kleptoparasite's success is dependent on the size or handling time of the prey taken by the host. These two variables are normally positively correlated (Amat & Aguilera 1990, Ens et al. 1990; for an exception, see Steele & Hockey 1995) and have been shown to influence both the host's risk of being attacked and the risk of losing the prey (e.g., Hopkins & Wiley 1972, Hulsman 1976, Brockmann & Barnard 1979, Barnard & Thompson 1985, Hackl & Burger 1988, Amat & Aguilera 1990, Steele & Hockey 1995, Ratcliffe et al. 1997; but see Dunn 1973, Hulsman 1984).

A large prey should be worth more than a small prey to both the kleptoparasite and the host. One would therefore expect the kleptoparasite to spend more effort trying to sequester a large prey and the host more effort trying to keep it. This may be the reason why Cormorants and mergansers struggle hard to retain big fish and why aerial chases by gulls of Starlings carrying big earthworms may last for more than a minute.

One way to increase one's gain from kleptoparasitism is to defend the hosts (or an area where hosts are feeding) from other kleptoparasitic individuals. This strategy has been observed in different kleptoparasitic associations: Herring Gulls and Whooper Swans (Källander 1975), gulls and Eiders (Ingolfsson 1969, Prys-Jones 1973), Herring Gulls and Tufted Ducks (this study), Black-headed gulls and Lapwings (Källander 1977, Barnard & Thompson 1985), Common Gulls and Oystercatchers (Triplet & Etienne 1986), Common Gulls and Bar-tailed Godwits (Vader 1979), Ring-billed Gulls, Bonaparte's Gulls and Grey Plovers, Dunlin (Payne and Howe 1976). Great Black-backed Gulls often try to monopolise fishing flocks of Cormorants or Goosanders and manage to do so when these are small. However, at large fishing flocks they fail to do so, but frequent intraspecific aggression tends to result in some spacing of the gulls. This spacing does not, however, prevent many gulls from simultaneously attacking the same host (pers. obs.).

Success rate as an index of the profitability of kleptoparasitism

In this paper, I have presented data on the success rates recorded for kleptoparasitic attacks on various hosts by the four gull species treated. Is success rate a good index of the profitability of kleptoparasitism? Isn't the relevant measure the parasite's net energy gain per unit of time? The answer to the second question is 'yes'. However, there seems to exist a positive relationship between the kleptoparasites' success rate and how frequently different associations occur. For instance, for the most frequent kleptoparasitic association in South Sweden, that between gulls and Lapwings, overall success rate was as high as 55 percent. In contrast, gulls' success rate when kleptoparasitising Curlews was only c.15% and this association was observed less than ten times. Although other factors, notably the energy content of the prey, may influence the frequency with which different associations occur, a positive relationship between success rate and frequency of occcurrence suggests that success rate may be used as a substitute for net energy intake rate or the profitability of the kleptoparasitic feeding method.

Is kleptoparasitism important in the feeding ecology of the four gull species in South Sweden?

Apart from the widespread kleptoparasitic association of Black-headed Gulls and Common Gulls (especially the former) with Lapwings and Golden Plovers, which may allow the gulls to subsist on food stealing alone (Källander 1977), superficially kleptoparasitism would often seem not to be very important in the gulls' economy compared with other feeding methods. Thus, the number of gulls engaged in kleptoparasitism of diving ducks along the coasts was normally very small in relation to that found in fishing harbours and at refuse dumps. However, this observation does not demonstrate that kleptoparasitism is an unimportant feeding method. First, it may be important for certain segments of a gull population. Second, as pointed out repeatedly above, the incidence of kleptoparasitism increases during periods of food scarcity and it is during such periods its importance should be evaluated. It is suggestive that some 20–30 Great Black-backed Gulls at Lake Vombsjön appear to base their economy in winter on stealing fish from the large flocks of Cormorants and Goosanders.

Regional differences

The literature reviewed above shows that in winter some species, which in South Sweden are parasitised by one or both of the two large gull species and not, or only rarely, by Common Gulls and Black-headed Gulls, seem to be used as hosts by the latter two species quite regularly in Continental Europe. Examples are Goosander, Tufted Duck and Coot. The main reason for this difference probably is that relatively few Common Gulls and Black-headed Gulls winter in Sweden, where Herring Gulls dominate numerically during the cold season. In South Sweden competition with the large gull species may also make kleptoparasitism less profitable for the smaller gulls, which in stead tend to feed in urban environments, such as at park ponds, etc.

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Sammanfattning

Uppsatsen behandlar fyra måsfåglars (skrattmås, fiskmås, gråtrut och havstrut) stöld av föda från andra arter, s.k. kleptoparasitism. Den baseras på iakttagelser gjorda i södra Sverige, främst Skåne, från slutet av 1950-talet till dags dato och kan ses som en slags katalog över kleptoparasitism hos de nämnda måsarterna. Utgångspunkt för redovisningen är de värdarter, som de behandlade måsfågelarterna setts utnyttja. Uppgifter presenteras om säsongsmässig förekomst av den aktuella formen

av kleptoparasitism, parasitens attackbeteende och värdartens metoder att undgå att förlora sitt byte. I flertalet fall redovisas också kleptoparasitens framgång, dvs andelen lyckade stöldförsök av samtliga gjorda, uttryckt i procent. För varje värdart refereras också relevant litteratur, som behandlar olika måsarters utnyttjande av denna. I den följande svenska sammanfattningen har dock dessa litteraturreferenser uteslutits. Förekomsten av kleptoparasitism mot de olika värdarterna i södra Sverige sammanfattas i ett Appendix, som också innehåller uppgifter om parasiternas attackframgång.

Värdarterna och de måsarter som setts utnyttja dem

Skäggdopping

Flertalet observationer härrör från Vombsjön, där upp mot 2000 skäggdoppingar födosöker under senhösten. Framför allt fiskmås, men i ringa mån också skrattmås och gråtrut, associerade sig regelbundet med fiskande doppingar. De mindre arterna torde i huvudsak ha utnyttjat fisk, som pressats upp mot ytan av doppingarnas dykaktivitet, men attacker av fiskmås mot doppingar med fisk iakttogs också, dock med låg framgång (två lyckade av totalt 18 attacker). I Centraleuropa tycks kleptoparasitism från fisk- och skrattmåsars sida mot övervintrande skäggdoppingar vara vanlig på vissa lokaler.

Storskarv

Såväl solitärt fiskande skarvar (vid kusten) som flockfiskande (såväl vid kusten som i insjöar) utsattes regelbundet för kleptoparasitism från grå- och havstrutar. Speciellt de stora fiskeflockar, som regelbundet kunde ses utanför Falsterbo om hösten, i Skälderviken under vintern, och i Vombsjön under framför allt senhöst och vinter, attraherade stora mängder trutar. Avstånden var dock oftast för stora för att trutarnas framgång skulle kunna avgöras. Därtill kom att en skarv med fisk ofta attackerades samtidigt av flera trutar, vilket resulterade i ett virrvarr av vingar. Materialet från Vombsjön antyder dock att cirka 20% av alla attacker var lyckade, såväl för grå- som havstrut (N=81 attacker). Under skarvfiskena var försök till inomartsparasitism mycket vanliga. När skarvar, som kommit upp med en stor fisk och ruschande över vattenytan försökte undkomma förföljande artfränder, utlöste detta nästan alltid attacker från trutarnas sida.

Sångsvan

Hur sångsvanar, som livnärde sig på sandmusslor *Mya arenaria* vid Öresundskusten, parasiterades av gråtrutar har tidigare beskrivits (Källander 1975). Trutarnas ofta mycket häftiga angrepp på svanarna resulterade i nära hälften av fallen (N=504) i att truten erövrade bytet.

Vigg och bergand

Vintertid övervintrar viggen talrikt (och berganden tämligen sällsynt) längs skånekusten, där den i stor utsträckning tycks utnyttja blåmusslor. Viggen är emellertid vintertid i huvudsak nattaktiv, men andelen viggar som dyker, ökar med sjunkande temperatur. I konsekvens härmed föreligger de flesta iakttagelserna av kleptoparasitism från kärva vinterperioder. Till skillnad från på kontinenten, där såväl fisk- som skrattmås utnyttjar viggar, parasiterades viggarna längs skånekusten nästan uteslutande av gråtrutar, vilka låg utspridda i viggflockarna och attackerade fåglar som kom upp med musslor i näbben. Viggarna försökte undkomma genom att dyka, varvid de ofta släppte sitt byte. I mer än hälften av de observerade attackerna lyckades gråtruten stjäla musslan.

Ejder

Associeringen av framför allt gråtrut (mera sällan havstrut) med ejder var en av de vanligast förekommande och iakttogs under alla månader, främst dock under perioder då ejdrarna uppträdde i större flockar, som under vintern och vårsträcket. Gråtrut sågs kleptoparasitera ejder ungefär 10 gånger oftare än vad havstrut gjorde. Även om trutar några få gånger sågs stjäla fisk (och fiskrens) från ejder, var ejdrarnas viktigaste föda utan tvivel blåmusslor. Gråtrutarnas framgång vid stöld av musslor var ganska hög, 38,5% (N=325 försök). Trutarna försökte ofta monopolisera en grupp dykande ejdrar eller en del av en större flock, något som beskrivits också från Scotland och Island.

Sjöorre och svärta

Jag gjorde endast en iakttagelse vardera av kleptoparasitism av svärta (en mindre flock gråtrutar, som attackerade en flock aktivt dykande svärtor utanför hallandskusten i slutet av juni) och sjöorre (två gråtrutar, som bevakade en flock på Skälderviken vintertid). Sannolikt förekommer kleptoparasitism av dessa arter oftare än vad mina iakttagelser

antyder, men båda arterna håller företrädesvis till långt från kusten (Nilsson 2005), vilket försvårar observationer.

Knipa

Knipflockar bevakades ganska regelbundet vintertid av gråtrutar, åtminstone under kärvare förhållanden. Trutarna sam omkring bland kniporna och attackerade då dessa kom upp med byte. Framgången var dock låg, 7%, om tre attacker mot knipor som fångat fisk utesluts. Många gånger sågs trutar ligga i knipflockar och uppmärksamt följa knipornas födosök men utan att attackera. Anledningen härtill och till den generellt låga framgången var säkerligen att knipan normalt lever på förhållandevis små byten, vilka snabbt kan sväljas.

Storskrak, småskrak och salskrak

Under senhösten uppträder mycket höga antal av storskrak i flera Syd- och Mellansvenska sjöar. Högstasiffror om 25 000 individer har rapporterats från Roxen (Druid & Tranesjö 1995) och 13 000 i Åsnen (O. Bondesson i brev). På dessa platser bildar de fiskeflockar om ibland åtskilliga tusen fåglar. Dessa attraherar regelbunder trutar, som försöker stjäla fisk. Också småskraken bildar ibland stora ansamlingar. Så är t.ex. fallet utanför Måkläppen vid Falsterbo i september–oktober (Roos 1982). Också dessa fiskeflockar attraherar stora mängder kleptoparasiterande trutar. Vintertid är båda arterna tämligen talrika längs de sydsvenska kusterna, vanligen med storskrakarna närmast stranden och småskrakarna längre ut.

Såväl stor- som småskrakar parasiterades av både havstrut och gråtrut, med havstrutar oftare associerade med storskrakar, och gråtrutar oftare med småskrak, en skillnad som är statistiskt säkerställd ($P<0{,}001$; vinterdata från Skånes sydkust, där båda trutarterna förekommer tillsammans). Både havstrut och gråtrut hade högre framgång vid parasitism av storskrak än vid parasitism av småskrak ($P<0{,}03$ resp. $P=0{,}05$). Havstrut hade högre framgång (53%, N=102 attacker) än gråtrut (28%, N=158 attacker) vid attacker mot storskrak medan ingen skillnad upptäcktes vid attacker mot småskrak, men antalet havstrutsattacker mot småskrak var lågt. Vid Vombsjön sågs också en del attacker av fiskmås mot flockfiskande storskrakar, dock med låg framgång (två av 18 attacker).

Vid kusten uppträdde trutars kleptoparasitism av storskrak i stor utsträckning under kärva vinterförhållanden, då storskrakarna koncentrerades till isfria områden. Under den stränga kylan i februari 1985 fiskade exempelvis storskrakar talrikt i Ystad hamn, som hölls öppen av de stora Polenfärjorna. Såväl inomartsparasitism som parasitism från havs- och gråtrutars sida var mycket intensiv. Skrakar försökte vanligen undgå att förlora sin fisk genom en snabb rusch längs vattenytan, förföljda både av artfränder, vilka t.o.m. klättrade på ryggen av den flyende skraken, och av trutar. Trots att havstrutar endast utgjorde 20% av hamnens trutar, lade de beslag på 88% av den fisk som stals från skrakarna. Dels tog de ofta över positionen närmast en flyende skrak från en gråtrut, dels tvingade de gråtrutar att ge ifrån sig stulna fiskar.

Sothöna

Åtta av nio iakttagelser av parasitism mot sothöns skedde under december–februari och sju av dem rörde gråtrutar. I de aktuella fallen dök sothönsen efter musslor och trutarna sam bland dem och attackerade när en sothöna kom upp med en mussla. Sothönsen försökte undkomma genom att rusa längs vattenytan, men 11 av 15 registrerade attacker var framgångsrika.

Strandskata

Blott två gånger iakttog jag kleptoparasitism mot strandskator, i juli respektive augusti. Vid båda tillfällena letade strandskatorna daggmask på bara åkrar. Vid det ena tillfället sågs fiskmåsar göra ett antal attacker mot tre strandskator, vid det andra var nio strandskator utspridda över en åker och attackerades av såväl skrattmåsar som gråtrutar när de funnit maskar. När en strandskata attackerades av en gråtrut sprang den undan och lämnade masken kvar på marken, men vid några tillfällen lyfte den med masken varvid den snabbt flög ifrån den förföljande truten. Strandskator, som lyckats svälja sitt byte, hotade attackerande skrattmåsar. Lyckade attacker sågs vid båda de nämnda tillfällena, men inget mått på måsfåglarnas framgång kan ges.

Ljungpipare och tofsvipa

Skratt- och fiskmåsars utnyttjande av framför allt tofsvipor, men också i stor utsträckning av ljungpipare, var den mest utbredda formen av kleptoparasitism i Sydsverige och förekom frekvent på åkermark och permanent gräsmark. Den kunde ses från sensommaren till dess de båda pipararterna lämnat landet, med en topp i Skåne i slutet av september och under oktober. Kleptoparasitism var vanlig

kalla vårar, då tofsvipor rastade i flock, medan den under varma vårar, då tofsviporna snabbt spred ut sig på häckningsreviren, kunde saknas helt. Parasitism mot ljungpipare om våren verkade nästan uteslutande förekomma under kyliga perioder, då ljungpipare rastade på gräsmarker. Beteendet har tidigare både beskrivits och analyserats i detalj.

Skratt- och fiskmåsar hade identisk framgång vid parasitism av tofsvipor (55%), medan fiskmåsar (52%) var effektivare än skrattmåsar (42%) vid parasitism av ljungpipare (P=0,002). Gamla måsar hade högre framgång än unga måsar, en skillnad som till stor del utjämnades under höstens gång.

Ytterligt få gånger sågs även gråtrutar parasitera på tofsvipor. Vid en av dessa var gråtrutarna utspridda bland tofsviporna på måsmanér och attackerade vipor som funnit en mask. Sådana attacker blev framför allt lyckosamma när vipan lämnade masken på marken och sprang undan, medan framgången var mycket sämre vid luftjakter.

Storspov

Nästan samtliga iakttagelser gjordes under kalla vårar, då storspovflockar rastade på gräsmark. I flertalet fall var den parasiterande arten skrattmås, blott i ett fall fiskmås. Måsarna attackerade storspovar när dessa halat upp en mask eller ibland redan när spovens rörelser visade att den var i färd med detta. Storspovarna använde tre olika metoder för att undgå att förlora sitt byte: (1) huka sig och rikta näbben mot måsen; (2) springa undan i zig-zag; och (3) ta till vingarna. Både attacker på marken och luftjakter resulterade ibland i att måsen lyckades stjäla masken (15% av fallen, N=155). Utbytet av att parasitera storspovar var dock lågt jämfört med att parasitera tofsvipor. Under 120 ”måsminuter” erhöll varje mås i medeltal blott 0,1 daggmask att jämföras med 0,27 maskar vid parasitism av tofsvipor.

Andra vadare

Några få gånger iakttogs ”opportunistiska” försök av skrattmåsar till stöld av daggmaskar från brushanar och grönbenor på översvämmade ängar. Brushanarna räddade dock sina byten genom att snabbt springa undan i zig-zag, medan grönbenorna omedelbart släppte masken då de attackerades.

Björktrast och rödvingetrast

Under 12 dagar om våren, alla utom en i april, noterades skrattmåsparasitism av björktrastar (och tillfälligtvis också rödvingetrastar). Detta skedde i samband med köldperioder, då trastarna rastade i stora flockar på gräsmark. Måsarna cirklade antingen lågt över de födosökande trastarna eller stod utspridda och bevakade dem uppmärksamt. I det förra fallet dök de snabbt ned när en trast halade upp en daggmask, i det senare fallet gjorde de en snabb anflygning. Båda resulterade ibland i att måsen lyckades erövra masken. En del attacker gav upphov till långa luftjakter. Trots att de stulna maskarna var mycket stora, torde måsarnas utbyte ha varit ganska lågt, nämligen 0,05 mask/mås/min.

Kråkfåglar

”Opportunistiska” attacker av fiskmåsar mot kajor och råkor, som funnit maskar, sågs ganska ofta i jordbrukslandskapet, men jag bedömde dem som ganska ointressanta. Av denna anledning registrerades utgången vid endast åtta av attackerna mot kaja och 15 mot råka; i samtliga fall blev de resultatlösa.

Stare

Starar utsattes för kleptoparasitism av fisk- och skrattmåsar i två helt olika situationer, dels i samband med köldinbrott om våren, då stararna under födosöket klumpade ihop sig i täta svärmar framför allt på gräsmark, dels i jordbrukslandskapet under hela hösten och i synnerhet i samband med plöjning och harvning (Figur 1). När måsarna utnyttjade täta starsvärmar om våren använde de endera av två metoder. Antingen flög de lågt över flocken och dök ned mot starar som funnit en mask eller så stod eller gick de inne i starflocken och gjorde korta anflygningar mot starar med mask. Stararna å sin sida försökte undkomma genom att springa eller flyga undan och i båda fallen göra tvära kast. Ibland resulterade måsarnas stöldförsök i långa luftjakter. Sådana var också vanliga i andra situationer, såväl vår som höst.

Höstetid iakttogs attacker mot starar ofta i samband med plöjning. När plogen passerat upphörde efter en stund måsarnas sökande efter maskar medan starar, när sådana fanns med, fortsatte att finna maskar bland tiltorna. De attackerades då av måsar. Också i andra situationer när starar födosökte på bara åkrar, ofta tillsammans med måsar, tofsvipor och ibland också ljungpipare, utsattes de för kleptoparasitism från måsarnas sida. Måsarnas framgång berodde mycket på omständigheterna. Långa luftjakter var positiva (från måsens synpunkt) i 38% av fallen (skrattmås) respektive 44% (fiskmås) mot

endast 16–19% av attacker till fots eller efter en kort anflygning.

Liksom vid andra former av kleptoparasitism hade bytesstorleken en mycket stor inverkan på kleptoparasitens framgång. Måsarnas framgång var större då stararna hanterade större byten (Figur 2).

Diskussion

Två former av kleptoparasitism mellan arter?

Jag har valt att skilja mellan ”opportunistisk” och ”reguljär” kleptoparasitism. Den förra är när olika arter utnyttjar samma slags föda och födosöker tillsammans, som exempelvis i anslutning till jordbruksredskap. När en fågel då finner ett större byte, kan det vara lönsamt för en annan individ att försöka stjäla bytet (”tillfället gör tjuven”). Av större intresse är de fall, där kleptoparasiten uppenbarligen lärt sig att känna igen vissa värdarter och associera sig med dessa, åtminstone när dessa födosöker aktivt. Exempel är skratt- och fiskmåsars utnyttjande av tofsvipor, gråtrutars av ejder, samt havs- och gråtrutars av skarvar och skrakar. Reguljär parasitism kombineras normalt inte heller med något eget aktivt födosök från parasitartens sida utan den förlitar sig på värdartens förmåga att finna byten (Payne & Howe 1976, Källander 1977, Buckley 1987; för ett exempel på motsatsen, se Ens et al. 1990).

I vilka situationer förekommer kleptoparasitism mellan arter?

Generellt skall man förvänta sig att kleptoparasitism skall förekomma när utbytet av parasitismen är större än av andra födosöksmetoder. Sådana situationer kan vara när en värdart gör föda tillgänglig, vilken parasiten eljest inte skulle ha tillgång till (dykande fåglar, vilka når föda på mycket större djup än måsar och trutar) eller när värdarten är långt skickligare än parasiten på att upptäcka dold föda (tofsvipor, ljungpipare, strandskator). Kleptoparasitism skall framför allt förväntas under perioder av födoknapphet (Furness 1987), något som stöds av att många av de här redovisade fallen förekom under kärva vinterförhållanden eller under kalluftsinbrott under våren.

Vilka faktorer påverkar en kleptoparasits framgång?

En viktig faktor, som påverkar en kleptoparasits framgång, är bytets storlek eller hanteringstid (dvs den tid det tar från det värden finner bytet tills det kan sväljas). Dessa två variabler är oftast positivt korrelerade, även om det kan finnas enstaka undantag. Ett bytes storlek har visats påverka såväl risken att en värd skall attackeras som risken att den skall förlora sitt byte.

Ett sätt att öka sin framgång vid kleptoparasitism kan vara att försvara ett antal värdar (eller ett område, där värdarna födosöker), något som iakttagits i ett flertal kleptoparasitiska sammanhang (bl.a. gråtrutar och sångsvanar, Källander 1975; trutar och ejdrar, Ingolfsson 1969, Prys-Jones 1973; gråtrutar och viggar, detta arbete; skrattmåsar och tofsvipor, Källander 1977, Barnard & Thompson 1985; fiskmåsar och strandskator, Triplet & Etienne 1986; fiskmåsar och myrspovar, Vader 1979).

Kan andelen lyckade attacker användas som ett mått på metodens lönsamhet?

I denna uppsats har jag presenterat en del data på hur stor andel av försöken till kleptoparasitism, där den parasiterande arten lyckats stjäla bytet från värden. Är detta ett bra mått på metodens lönsamhet? Borde man inte i stället jämföra nettoutbytet av kleptoparasitism med motsvarande för andra födosöksmetoder? Det senare vore säkert att föredra, men det faktum att det tycks finnas ett positivt samband mellan hur ofta en viss typ av kleptoparasitism uppträder och kleptoparasitens framgång, mätt som procenten lyckade attacker, gör att det senare måttet antagligen med fördel i många fall kan användas som en ersättning för det mer svårmätta nettoutbyte.

Är kleptoparasitism viktig i de fyra måsarternas näringsekologi?

Först kan konstateras att skrattmåsar under vissa årstider tycks kunna livnära sig uteslutande genom att parasitera på tofsvipor. Ytligt betraktat förefaller dock kleptoparasitism många gånger vara ett ganska betydelselöst näringsfång jämfört med andra metoder att skaffa sig föda. Antalet trutar inbegripna i parasitism mot dykänder längs kusten var t.ex. många gånger ringa jämfört med antalet i hamnar och på soptippar. Detta utesluter dock inte att kleptoparasitism kan ha betydelse. För det första kan den ha varit betydelsefull för en del av truppopulationen. För det andra ökar omfattningen av kleptoparasitism under perioder av födobrist, och det är under sådana perioder som dess betydelse skall utvärderas.

Appendix. The host species, and the gull species observed kleptoparasitising them in South Sweden. The gull species are abbreviated as follows: GB = Great Black-backed Gull, HG = Herring Gull, CG = Common Gull and BhG = Black-headed Gull. Gull species seen to parasitise a particular host only occasionally are in parentheses. Comments refer to how frequently the host was parasitised by its main kleptoparasite(s). Success rates are also indicated. For scientific names, see text.
De olika värdarterna och de måsarter som sågs kleptoparasitera dem. GB = havstrut, HG = gråtrut, CG = fiskmås och BhG = skrattmås. Måsarter som endast tillfälligtvis setts kleptoparasitera en viss värdart ges inom parentes. Kommentarerna avser hur ofta en viss värdart utnyttjades av sin huvudsakliga parasitart (-arter). Kleptoparasiternas framgång (procent lyckade försök) anges också. För arternas vetenskapliga namn, se texten.

Host species *Värdart*	Kleptoparasite *Kleptoparasit*	Comments on occurrence and kleptoparasites' success rates *Kommentarer*
Black-throated Diver *Storlom*	GB, HG	Only observed a few times. Success rate unknown *Få iakttagelser, framgång okänd*
Great Crested Grebe *Skäggdopping*	(HG), CG	May occur slightly more often than observations suggest but success rate apparently low *Kan förekomma oftare än observationerna antyder men framgången uppenbarligen låg*
Great Cormorant *Storskarv*	GB, HG, (CG)	Common both inland (all seasons) and at the coast (autumn,winter). Success rate c.20% *Vanligt förekommande i inlandet (alla årstider) och vid kusten (höst, vinter). Framgång c.20%*
Whooper Swan *Sångsvan*	HG	Perhaps occurs rather frequently along sandy coasts, but may have become rarer in recent decades as Whooper Swans have increasingly turned to grazing inland. Success rate almost 50% *Förekommer ev. ganska ofta längs sandiga kuster men kan ha blivit ovanligare i takt med att sångsvanar i ökad utsträckning betar i inlandet. Framgång nästan 50%*
Tufted Duck *Vigg*	HG (BhG, CG)	Along the coast in harsh winter conditions. Success rate seemed to be around 50% *Längs kusten under kärva vinterförhållanden. Framgång runt 50%*
Greater Scaup *Bergand*	HG	Occurrence as for Tufted Duck. No data on success rate *Förekomst som för vigg. Inga data om framgång*
Eider *Ejder*	GB, HG	Very common, especially in winter and during the Eider's spring migration. Success rate just <40% *Mycket vanligt förekommande, särskilt vintertid och under ejderns sträckperiod om våren. Framgång strax under 40%*
Velvet Scoter, Black Scoter *Svärta, sjöorre*	HG	Only observed once for each species; probably occurring more often than observations suggest. No data on success rate *Endast en observation för vardera arten, men förekommer ev. oftare en iakttagelserna antyder. Framgång okänd*
Common Goldeneye *Knipa*	HG	Seen quite frequently at the coast in harsh winter conditions. Success rate apparently very low *Ofta längs kusten under kärva vinterförhållanden. Framgången uppenbarligen mycket låg*

forts.

Appendix forts.

Host species *Värdart*	Kleptoparasite *Kleptoparasit*	Comments on occurrence and kleptoparasites' success rates *Kommentarer*
Goosander *Storskrak*	GB, HG, (CG)	Common, mostly in late autumn and winter. Success rate c.50% (GB) and 30% (HG) *Vanligt förekommande, särskilt höst och vinter. Framgång c.50% (GB) och 30% (HG)*
Red-breasted Merganser *Småskrak*	GB, HG	Almost year-round, especially by HG. Success rate 15–20% *Nästan året runt, särskilt av HG. Framgång 15–20%*
Eurasian Coot *Sothöna*	HG, (BhG,CG)	Seen a few times in winter. Success rate c.70% (HG) but few attacks recorded *Några få gånger vintertid. Framgång (HG) c.70% men få attacker registrerade*
Oystercatcher *Strandskata*	BhG, CG, HG	Only seen twice when Oystercatchers were feeding on earth worms. No data on success rate *Endast två gånger, då strandskator livnärde sig på daggmask. Inga data om framgång*
Northern Lapwing *Tofsvipa*	BhG, CG, (HG)	Widespread and common. Success rate c.55% (BhG, CG) *Vanligt förekommande. Framgång c.55%*
Golden Plover *Ljungpipare*	BhG, CG	Widespread and common in autumn. Success rate c.40–50% *Vanligt höstetid. Framgång c.40–50%*
Curlew *Storspov*	BhG, CG	Seen only a few times when Curlew flocks stopped over during spring migration. Success rate c.15% (BhG) *Endast när storspovar rastade i kallt väder om våren. Framgång c.15%*
Ruff, Wood Sandpiper *Brushane, grönbena*	BhG	Opportunistic attacks, flooded meadows in spring *Opportunistiska attacker på blöta ängar om våren*
Fieldfare *Björktrast*	BhG	In cold weather during spring migration. No data on success rate but gulls' intake rate very low *I kallt väder under vårflyttningen. Inga data om framgång men litet energiintag per tidsenhet*
Rook, Western Jackdaw *Råka, kaja*	CG	Opportunistic attacks in connection with farming operations. Success rate zero but sample small *Opportunistiska attacker i samband med jordbruksverksamhet. Framgång ingen*
Common Starling *Stare*	BhG, CG, (HG)	Regularly in cold weather during Starlings' spring migration, more opportunistically during farming operations in autumn. Success rate depending on gulls' tactic varying from c.16% to c.45% *Regelbundet vid kallt väder under starens sträckperiod om våren, mer opportunistiskt i samband med jordbruks-aktivitet om hösten. Framgång beroende av attackmetod, 16–45%*