# INTERACTIONS BETWEEN HERRING AND LESSER BLACK-BACKED GULLS FEEDING ON REFUSE

NICOLAAS A. M. VERBEEK

ABSTRACT.—The interactions among Lesser Black-backed Gulls and Herring Gulls during the breeding season while feeding on a refuse dump on Walney Island, England were analyzed. Herring Gulls were found to be more aggressive than Lesser Black-backs, and they were equally aggressive toward Lesser Black-backs and Herring Gulls. It is suggested that Lesser Black-backs are more timid than Herring Gulls and avoid being pecked at by them. Most of the Herring Gulls (77%) found their own food, 95% of the Lesser Black-backs stole theirs. In contrast to Herring Gulls, Lesser Black-backs rarely dug for food and those that fed independently (5%) found less food than Herring Gulls. Lesser Black-backs were very efficient in stealing food, mostly from Herring Gulls. It is suggested that the number of Lesser Black-backs feeding on the dump is dependent on the number of Herring Gulls. *Department of Zoology, Animal Behaviour Research Group, Oxford, England. Present address: Department of Biology, Simon Fraser University, Burnaby, B.C. V5A 1S6, Canada.* Accepted 5 April 1976.

THE Herring Gull (*Larus argentatus*) and the Lesser Black-backed Gull (*L. fuscus*) are closely related species (Mayr 1963) that on occasion produce fertile hybrids (Tinbergen 1953). The species are very similar in body dimensions (Barth 1975). These gulls occupy different food niches (Brown 1967, Shaffer 1971) but considerable overlap occurs on certain feeding substrates (Hunt and Hunt 1973). Given this close similarity one might expect either extreme competition and aggression, or the avoidance thereof because each species uses the common substrate in a different way. This paper examines these possibilities in a situation where both species feed simultaneously on a refuse dump.

The study was made on Walney Island, Cumbria, England, in 1973–74. Both species of gulls nest on the south end of the island, about 3 km from the dump. Shaffer (1971) showed that roughly three times more Herring Gulls than Lesser Black-backs frequented this dump, and he suggested that the Herring Gulls "simply drive the Lesser Black-backs away." This implies severe competition and aggression, which the detailed observations set out in this paper do not support.

## METHODS

To analyze the feeding behavior I watched gulls of both species as they approached the dump in flight and I recorded their subsequent activities. Each gull was chosen arbitrarily as it approached the dump, ca. 10 m off the ground and about 15 m from the feeding area proper. The moment I focused on a gull I followed it until the bird landed to stand, feed, rob another gull, or began to chase another gull in flight.

Food was placed on the dump in heaps leveled flat by a bulldozer, and on the down slope (face) of the dump. I arbitrarily divided a heap of refuse into a top and a bottom zone and timed how long each species spent in these two zones from the moment a bird landed until it left. Simultaneously I also noted the number of times these birds pecked other gulls or were pecked by them in each zone. I followed the same procedure on the leveled top of the dump which I divided into three zones, the lip (ca. 2 m wide), the middle (ca. 5 m wide), and the edge (ca. 5 m wide). These zones ran parallel to the face of the dump. I collected no data on the face of the dump because I could not park near enough to it. I watched the gulls with and without binoculars (8 × 40) from a car parked some 30 m away.

## RESULTS

*Feeding behavior on the dump.*—Herring and Lesser Black-backed Gulls fed on the dump in quite different ways (Table 1). Most (77%) of the Herring Gulls ap-

TABLE 1

SUBSEQUENT ACTIVITIES, AND THEIR FREQUENCY, OF HERRING GULLS (HG) AND LESSER BLACK-BACKED GULLS (LBG) APPROACHING THE DUMP IN FLIGHT

| | | Landing | | | | | |
|---|---|---|---|---|---|---|---|
| | | Robbing | | | | | |
| Species | Total number | Success N (%) | No success N (%) | Unknown N (%) | Standing N (%) | Feeding N (%) | Chasing N (%) |
| HG | 76 | | 6 (7.8) | | 11 (15.6) | 59 (76.6) | |
| LBG | 126 | 14 (11.1) | 31 (24.6) | 16 (12.7) | 27 (21.4) | 6 (4.8) | 32 (25.4) |

proaching the dump in flight landed to feed, while only 5% of the Lesser Black-backs did so (Table 1). On landing these birds began to feed on their own within a few seconds. Some birds (16% of the Herring Gulls and 21% of the Lesser Black-backs) landed merely to stand among other feeding gulls. These percentages are not significantly different ($\chi^2 = 1.08$, df 1). These birds carefully watched for other gulls with food which they then tried to steal, either by snatching it or by supplanting attacks. Many of the gulls that approached the dump in flight did not land, but circled overhead looking for an opportunity to rob the food of a gull on the ground. Almost half of the Lesser Black-backs (48%) used this feeding method, but only 8% of the Herring Gulls did (Table 1). Lastly, while flying back and forth over the dump, 25% of the Lesser Black-backs watched for other gulls flying from the dump with large food items. Once such a departing gull was spotted, the Lesser Black-backs chased it. Herring Gulls also chased, but more rarely, and none of the 76 birds I watched approached the dump to chase (Table 1). In summary, 77% of the Herring Gulls approached the dump to feed on their own, while 95% of the Lesser Black-backs did so to steal.

*Feeding success.*—In those birds that landed to feed on their own (Table 1), I counted the number of successful pecks (those followed by swallowing) over a period of time. Each bird was followed until it flew away, moved out of sight, or until it found a large food item it could not swallow immediately. This food item was not included in the total number consumed. I only gathered data from birds on the edge because they were clearly visible. In this zone most food particles are small. Lesser Black-backs found significantly fewer items per minute ($U = 2.14$) than Herring Gulls (Table 2), which might well explain why Lesser Black-backs feed little on their own in the first place.

In contrast to Herring Gulls, Lesser Black-backs rarely dug for food on the dump. By digging I mean removing with the bill such inedible items (often large ones) as folded newspapers, rags, and pieces of cardboard to expose food. In 42.3 minutes 40

TABLE 2

FEEDING RATE OF THE HERRING GULL (HG) AND THE LESSER BLACK-BACKED GULL (LBG) FORAGING ON THE EDGE OF THE DUMP

| Species | N | Number of pecks[1] | Total time (min) | Mean number of pecks/min[2] |
|---|---|---|---|---|
| HG | 40 | 113 | 46.6 | 2.43 |
| LBG | 43 | 92 | 55.0 | 1.67 |

[1] Those followed by swallowing.
[2] By calculating the pecking rate per minute for each individual and averaging these, the mean for HG is 2.69, for LBG 1.81. These results are significantly different from each other (Mann-Whitney test, $U = 2.14$).

TABLE 3
THE PROPORTION OF BIRDS CARRYING LARGE FOOD ITEMS FROM THE DUMP WITHOUT BEING PURSUED, AND THOSE BEING PURSUED

| Species | N | Pursued | Not pursued | % pursued |
|---|---|---|---|---|
| Herring Gull | 102 | 66 | 36 | 65 |
| Lesser Black-backed Gull | 133 | 48 | 85 | 36 |

Herring Gulls moved 150 objects; 19 Lesser Black-backs moved only 6 objects in 22.7 minutes. Herring Gulls improve on this habit as they mature (Verbeek 1977a). Although Herring Gulls spend part of the time digging, this lost time is compensated for by finding extra (hidden) food. Apparently the digging habit allows Herring Gulls, at least on the edge of the dump, to find significantly more small food items per unit time than do Lesser Black-backs.

I have no direct evidence on the success rate of those birds that land to stand in order to steal a meal if possible, but I did record instances where I happened to see either species stealing food from each other. These were not instances where the thief landed to rob. Very likely these were birds standing and waiting for an opportunity to steal. I only recorded positive scores. As Herring Gulls were much more numerous on the dump than Lesser Black-backs, and the frequency of birds standing (Table 1) was not significantly different for each species, one would have expected many more instances of Herring Gulls stealing from Lesser Black-backs than vice versa. However I recorded 37 Lesser Black-backs successfully stealing food from Herring Gulls, and only 16 cases in the reversed situation. Apparently, therefore, Lesser Black-backs are the better thieves.

Robbing food by landing quickly near a Herring Gull that has found it appears to be a profitable way of feeding for Lesser Black-backs. They were successful 31% of the time (Table 1). The few Herring Gulls that practiced this form of robbing were not successful. Food thus obtained may be stolen from single birds or from a huddle of birds. A huddle of birds frequently forms around a Herring Gull exposing food. The ensuing melee attracts birds from the air as well as those standing about. When a huddle forms it usually concerns a large food item and if that can be stolen successfully, no further searching for food may be necessary. The huddles are usually composed of both species, but because of the chaos I have no data on the ratio of each species involved. A conservative estimate would be eight Herring Gulls for each Lesser Black-back. I did record the species that emerged with food from such huddles. If my estimate is correct, one would expect 8 times more Herring Gulls to emerge with food than Lesser Black-backs, but the score obtained was 14 Herring Gulls and 35 Lesser Black-backs. Again, Lesser Black-backs appear to be very successful in stealing from Herring Gulls. In a tug-of-war between Herring Gulls and Lesser Black-backs over some food item, there was little difference in the success of either species (13 wins for Herring Gulls, 17 for Lesser Black-backs). This is somewhat surprising because Herring Gulls are heavier birds and therefore presumably stronger.

Pursuing a bird in flight and forcing it to drop food is another way in which gulls obtain food (Meinertzhagen 1959, Grant 1971). I followed a number of Lesser Black-backs and Herring Gulls that flew from the center of the dump with food and I recorded whether or not they were subsequently chased. Only 36% of the Lesser Black-backs were chased, compared to 65% of the Herring Gulls (Table 3). Evi-

TABLE 4

SUCCESS IN PURSUITS IN WHICH ONLY ONE HERRING GULL OR LESSER BLACK-BACKED GULL PURSUES ANOTHER OF EITHER SPECIES

| Success-ful | LBG pursues | | | HG pursues | | |
|---|---|---|---|---|---|---|
| | HG | LBG | Total | HG | LBG | Total |
| | N (%) | N (%) | N (%) | N (%) | N (%) | N (%) |
| Yes | 51 (43) | 18 (21) | 69 (34) | 1 (10) | 2 (10) | 3 (10) |
| No | 67 (57) | 68 (79) | 135 (64) | 9 (90) | 17 (90) | 26 (90) |
| Total | 118 | 86 | 204 | 10 | 19 | 29 |

dently, Herring Gulls are discriminated against. Considering that Herring Gulls on the dump outnumbered Lesser Black-backs 3 to 1, one might have expected (all else being equal) 399 Herring Gulls to have departed with food instead of only 102 (Table 3). Instead, about four Lesser Black-backs left for each three Herring Gulls. Many of the Herring Gulls had probably already lost their food before they had a chance to depart with it. Others may have opted for not flying away to avoid being pursued, thereby increasing the risk of losing the food on the ground.

On some days I concentrated on aerial chases over the dump, trying to record as many as possible. The success of the chase (i.e. whether the chaser obtains the food) depends on which species is chasing and which one is being chased. Taking all successes regardless of the species pursued (by a single bird), Lesser Black-backs were successful in 34% of the chases, compared to 10% for Herring Gulls (Table 4). Lesser Black-backs had significantly ($\chi^2 = 10.07$, df 1) more success when chasing a Herring Gull than when chasing another Lesser Black-back. Herring Gulls had an equal chance of success ($\chi^2 = 0.47$, df 1) when pursuing either species. In comparing the number of Herring Gulls and Lesser Black-backs leaving the dump with food (Table 3) with the number that were being pursued by Lesser Black-backs (Table 4), it appears that Lesser Black-backs preferred to chase Herring Gulls ($\chi^2 = 7.20$, df 1). Table 4 shows that far more single Lesser Black-backs than Herring Gulls chase other gulls of either species, which agrees with Table 1.

Often single gulls are pursued by several birds. I have counted as many as 15 gulls in pursuit and at times more are involved. The success per pursuer fell progressively from 31% for a single bird to 7.5% when 8 birds were involved in a chase (Fig. 1). Similar data are available for Arctic Terns (*Sterna paradisaea*) and Common Terns (*S. hirundo*) pursued by Laughing Gulls (*L. atricilla*) (Hatch 1970). In that study the success per chase was higher than what I recorded and fell progressively from 45% for a single bird to about 14% when eight birds were in pursuit.

The success per chase (i.e. the chance that any gull will succeed, or vice versa that the bird which is being pursued will lose its food item) increases rapidly at first to level off at about 80%. These data agree with those of Hatch (1970) except that the success per chase in my study never reached 100%. In fact it appears that if too many gulls ($N > 9$) participate the success per chase declines to about 70%. Apparently as more birds join in they interfere with each other and so improve the chances of the pursued bird keeping its food.

*Flightlines in conjunction with dumping.*—Both species returned to the colony from the dump in larger numbers shortly after refuse was dumped than at other times. If Lesser Black-backs obtain food more quickly because they do not first have to dig for it and because they successfully steal much if not most of it from Herring

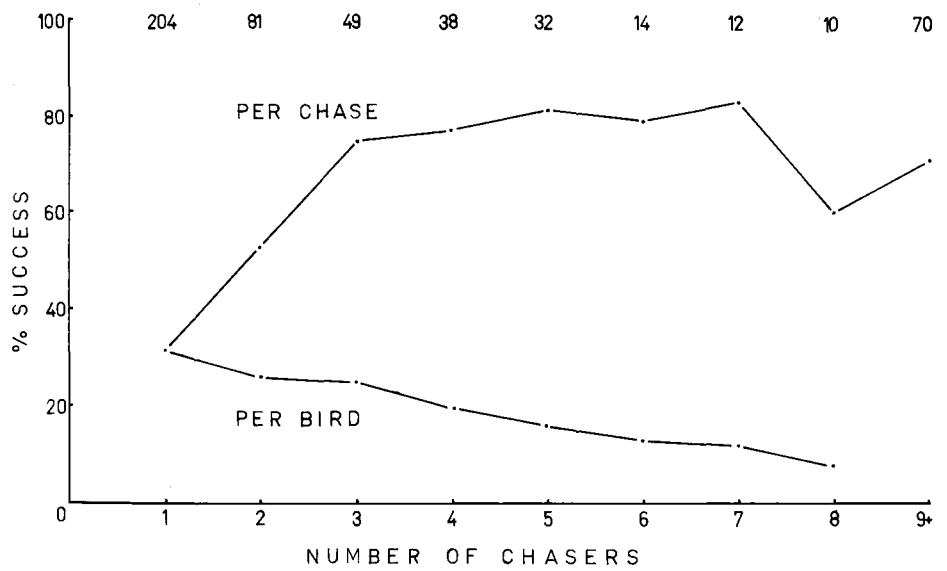


Fig. 1. Percent success of chases of Herring Gulls and Lesser Black-backed Gulls pursuing each other in aerial pursuits. The number of pursuers varied from 1 to 9 + . The top row of figures represents the number of chases recorded.

Gulls, one would expect them to stay a shorter time on the dump than the Herring Gulls following dumping of new refuse. Consequently the proportion of Lesser Black-backs among birds returning to the colony should rise following dumping. To verify this I sat close to the colony from where I could see the refuse trucks arriving on the dump in the distance. I counted the number of each species per unit time as they returned from the dump and I recorded the moment when each truck unloaded. As expected, the proportion of Lesser Black-backs among the returning birds did indeed rise (Fig. 2). The results of 24 July are less convincing than for the other days shown, but this is probably because of the scattered arrival of the trucks on that day. I cannot account for the large peak between 1500 and 1510 on 18 July, unless perhaps the bulldozer was active before the trucks arrived.

TABLE 5

MEDIAN DURATION OF TIME SPENT BY GULLS IN VARIOUS PARTS OF THE DUMP

| Feeding zones | Herring Gull N | Herring Gull Median time (sec) | Herring Gull Diff. sig.[1] | Lesser Black-backed Gull N | Lesser Black-backed Gull Median time (sec) | Lesser Black-backed Gull Diff. sig.[1] | Diff. sig. between[1] |
|---|---|---|---|---|---|---|---|
| Flat area | | | | | | | |
| lip | 46 | 48 | Yes | 39 | 14 | Yes | Yes |
| middle | 28 | 156 | No | 42 | 56 | Yes | Yes |
| edge | 24 | 97 | No | 23 | 60 | No | No |
| Heaps | | | | | | | |
| top | 40 | 53 | No | 30 | 13 | No | Yes |
| bottom | 38 | 56 | | 26 | 25 | | No |

[1] Median test in Siegel 1956, $\chi^2$ with one degree of freedom, $P = 0.001$.

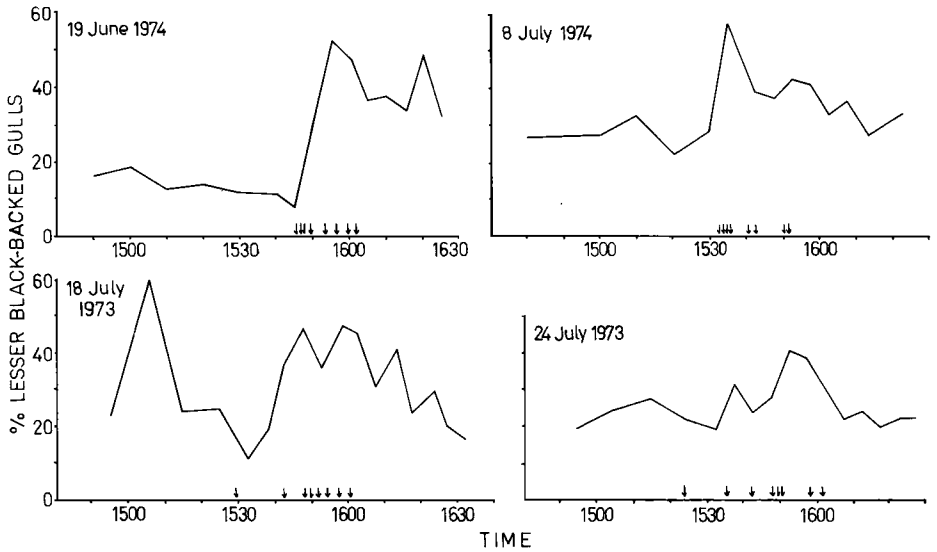


Fig. 2. The percentage of Lesser Black-backed Gulls among all gulls counted returning to the colony from the Walney dump plotted in relation to the time at which each of 8 refuse trucks (↓) unloaded.

*Time expenditure*.—Each truck has in the back a large screw that transports the refuse into its hold. Some refuse becomes stuck in this screw and has to be removed by hand. This cleaning sometimes occurred beyond the usual dumping ground and left a little pile of material there. Lesser Black-backs were usually first to land on these piles. Shortly after the Herring Gulls arrived, the Lesser Black-backs moved to the outside and soon left altogether. This replacement of one species by the other occurred without fighting or other signs of overt aggression in 22 ± 8.0 seconds (N = 17), counting from the time the first Lesser Black-back landed.

The refuse trucks usually dumped on the center of the dump and the bulldozer then pushed the refuse over the lip. Frequent forward and backward riding and

TABLE 6

THE FREQUENCY WITH WHICH HERRING GULLS AND LESSER BLACK-BACKED GULLS PECKED NEIGHBORING HERRING GULLS IN DIFFERENT ZONES OF THE DUMP[1]

| Feeding zone | HG pecks HG | | | LBG pecks HG | | |
|---|---|---|---|---|---|---|
| | N | Time (min) | Pecks/bird/ min[2,3] | N | Time (min) | Pecks/bird/ min[2,3] |
| Flat area | | | | | | |
| lip | 43 | 52.0 | .58 | 29 | 16.7 | .09 |
| middle | 30 | 97.3 | .31 | 33 | 38.6 | .06 |
| edge | 24 | 53.8 | .11 | 18 | 28.6 | .00 |
| Heaps | | | | | | |
| top | 33 | 46.3 | .81 | 17 | 4.5 | .00 |
| bottom | 38 | 57.8 | .21 | 23 | 14.5 | .27 |

[1] The individuals belonging to the underlined species in this and following tables are the ones I followed over time.
[2] The rate per minute with which HG and LBG peck HG is significantly different ($P < 0.05$) on the lip, edge, and top (Mann-Whitney $U$-test corrected for ties).
[3] Comparison of the pecking rate between any two zones on the flat area and on the heaps (within columns) is not significant.

TABLE 7

THE FREQUENCY WITH WHICH HERRING GULLS AND LESSER BLACK-BACKED GULLS ARE PECKED AT BY NEIGHBORING HERRING GULLS IN DIFFERENT ZONES OF THE DUMP

| Feeding zones | HG pecked at by HG | | | LBG pecked at by HG | | |
|---|---|---|---|---|---|---|
| | N | Time (min) | Pecked at/ bird/min[1,2] | N | Time (min) | Pecked at/ bird/min[1,2] |
| Flat area | | | | | | |
| lip | 43 | 52.0 | 1.00 | 29 | 16.7 | .59 |
| middle | 30 | 97.3 | .37 | 33 | 38.6 | .66 |
| edge | 24 | 53.8 | .21 | 18 | 28.6 | .03 |
| Heaps | | | | | | |
| top | 33 | 46.3 | 1.34 | 17 | 4.5 | .24 |
| bottom | 38 | 57.8 | 1.07 | 23 | 14.5 | .31 |

[1] The rate with which HG and LBG in the same zone are pecked at is significantly different ($P < 0.05$) on the top and the bottom (Mann-Whitney $U$-test corrected for ties).

[2] Comparison of the rate of being pecked at between any two zones on the flat area and on heaps (within columns) is significantly different for LBG on the edge and the middle.

turning of the bulldozer's treads packed the refuse, fragmented the food particles, and ground them into the surface. The degree of packing, grinding, and fragmentation increased from the lip to the edge, so potentially more food and food of larger particle size were thus available on the lip than on the edge. Consequently, the density of birds was greatest near the lip and decreased away from it.

Both species spent significantly less time on the lip than on the middle (Table 5), i.e. the turnover rate was greater on the lip than on the middle. Lesser Black-backs also spent significantly less time on the lip than on the edge. The two species do not differ significantly in time spent on the middle and the edge. On heaps, food is probably equally available on the top and on the bottom. Neither species spent significantly more time on the bottom of a heap than on the top (Table 5). The overall trend was for Lesser Black-backs to spend less time than Herring Gulls in each zone. The obvious question is: why?

*Pecking interactions*.—One would expect, for instance, more aggressive interactions on the lip than on the edge because the birds are closer together on the lip. This expectation is confirmed in Tables 6 and 7. However only the rates with which Lesser Black-backs were pecked at by Herring Gulls on the middle and the edge (Table 7) are significantly different. Nevertheless the pattern of gradual decrease in the rate of interactions from the lip to the edge and to a lesser degree from the top to the bottom is repeated four times in Tables 6 and 7. This considerably strengthens the idea that biologically the trends shown are important.

Pecking interactions among gulls on the dump are potentially of two kinds. Each gull I watched feeding on the dump could peck another gull of either species or be pecked by one. This gives a total of eight types of interaction (Table 8). Regardless of the proportion of each species present on the dump, and all else being equal, a Herring Gull and a Lesser Black-back have an equal chance of pecking a Lesser Black-back. Similarly they have an equal chance of pecking a Herring Gull. This may not be immediately obvious to the reader. If we suppose that a Herring Gull walks past $x$ other Herring Gulls and $y$ Lesser Black-backs, and that it pecks each one once, the total number of pecks is $x + y$. Similarly, all else being equal, a Lesser Black-back walking past those same birds delivers a total of $x + y$ pecks. It follows that, all else being equal, a Herring Gull and a Lesser Black-back should be seen

TABLE 8

THE NUMBER OF AGGRESSIVE ENCOUNTERS BETWEEN HERRING GULLS AND LESSER BLACK-BACKS FEEDING ON THE DUMP[1]

| Type of interaction | Number of encounters | Type of interaction | Number of encounters |
|---|---|---|---|
| HG pecks HG | 117 | HG pecks LBG | 1 |
| LBG pecks HG | 49 | LBG pecks LBG | 6 |
| HG pecked by HG | 148 | HG pecked by LBG | 5 |
| LBG pecked by HG | 120 | LBG pecked by LBG | 6 |

[1] See text for further details.

pecking a Herring Gull the same number of times if followed for the same length of time. As explained earlier, I could not watch the Lesser Black-backs for as long as the Herring Gulls in all zones. In order to make a comparison possible, the observations on Lesser Black-backs were adjusted as follows. In each of the 5 zones the total number of aggressive encounters for the Lesser Black-backs was recalculated to the same length of time the Herring Gulls in that zone had been watched. Thus I obtained a new set of 5 numbers for each of the 4 types of interaction in which the Lesser Black-back was the gull followed. For each type of interaction, the 5 numbers obtained were then added to give the total number of encounters for that interaction (Table 8). For the interactions in which the Herring Gull was the gull followed, the total number of encounters for each interaction was derived in the same way, except that the observations needed no adjustment. It is clear that my original supposition "all else being equal" does not hold (Table 8). Herring Gulls pecked significantly more Herring Gulls (117 times) than Lesser Black-backs did (49 times) ($\chi^2 = 27.9$, df 1). The data shown for Herring Gulls and Lesser Black-backs pecking Lesser Black-backs are insufficient for statistical treatment. It would appear that Herring Gulls are more aggressive than Lesser Black-backs. Insufficient data on the right side of Table 8 (1 versus 6 pecks) does not allow a definite statement for the alternative possibility, that each species is more aggressive intra- than interspecifically (but see below).

All else being equal, a Lesser Black-back and a Herring Gull should have an equal chance of being pecked at by a Herring Gull or by a Lesser Black-back. This is confirmed for the Herring Gull in the lower two values in Table 8. Here again, the low values (5 versus 6) for Lesser Black-backs pecking at either species are suggestive but should be treated with caution. Apparently Herring Gulls are equally aggressive against their own species as against Lesser Black-backs. The same may be true where Lesser Black-backs are the aggressors. This conclusion contradicts the alternative possibility above.

It is possible that Lesser Black-backs avoid being pecked at by moving out of the way of an approaching Herring Gull. The low values on the right side of Table 8 would support this. On the other hand Herring Gulls and Lesser Black-backs were pecked equally often by neighboring Herring Gulls (148 and 120 times respectively) ($\chi^2 = 2.92$, df 1). This apparent contradiction can be resolved if we consider that the Lesser Black-backs I watched feeding over time represented only those birds that sought their own food (5%, Table 1). These birds were apparently more aggressive than most Lesser Black-backs and they let themselves be pecked at by a Herring Gull as often as Herring Gulls do, while continuing to feed ($\chi^2 = 0.15$, df 1).

## DISCUSSION

The feeding behavior of the Herring Gull and the Lesser Black-back and the interactions among them while feeding together on a dump are complex. Each species exploits the food source in a different way

Several lines of evidence show Lesser Black-backs to be less aggressive than Herring Gulls when the two species feed together. (1) On small piles of food Lesser Black-backs go away as soon as Herring Gulls move in. (2) The great majority of Lesser Black-backs avoid being pecked at by Herring Gulls (Table 8). (3) Until Lesser Black-backs have eggs in the nest they generally do not stand up to invading Herring Gulls (Tinbergen, pers. comm.). As an apparent consequence, Lesser Black-backs spend less time on the surface of the dump than Herring Gulls, and this is not because they are more efficient in seeking their own food (Table 2).

The ability to dig allows Herring Gulls to obtain more of the total food source on the dump than do Lesser Black-backs, which by and large find only the exposed items. This is an important difference between the species. In addition, in parts of the dump where food is most abundant Lesser Black-backs spend least time (Table 5); some of the food potentially available to them goes therefore unused. Those Lesser Black-backs that seek their own food appear to be at a disadvantage when competing with Herring Gulls. This may explain why so few Lesser Black-backs feed independently.

Once the food on the surface is gone, Lesser Black-backs are dependent on Herring Gulls for digging out the rest. Much of the hidden food is subsequently stolen by cleptoparasitic Lesser Black-backs, either on the ground or in aerial pursuits. In this study 95% of the Lesser Black-backs stole their food (Table 1). Their victims were mainly Herring Gulls (Table 4). Many Lesser Black-backs pursued by conspecifics were probably birds that had stolen the food they were carrying in the first place. One wonders why Herring Gulls do not rob Lesser Black-backs more often. I think the answer is that Herring Gulls are slower than Lesser Black-backs and in aerial pursuits they are less successful (Table 4). This is related to their wing loading (Verbeek 1977b).

As much of the stolen food consists of large items, successful thieves are more quickly satisfied and they can return to the colony more quickly than birds that seek their own food. Also, birds whose food is stolen (mainly Herring Gulls) have to spend extra time and energy finding new food. Lesser Black-backs were successful in 1 out of 3 chases and in 1 out of 3 attempts to steal food on the ground. This success is reflected in their quick return to the colony (Fig. 2), which might allow their mates to fly to the dump and to be there in time to profit from the same dumping session. This would allow a greater number of Lesser Black-backs to visit the dump than thought without upsetting the one to three ratio of Lesser Black-backs to Herring Gulls present there. I do not think this is the case. First, food is not continuously available on the dump because the refuse trucks tend to come together and there are long periods when no refuse is dumped at all. This produces a situation of feast and famine. Second, human disturbance on the dump often prevents the gulls from feeding. The time for most successful stealing is limited to those periods when refuse is being dumped and shortly thereafter. Food is most abundant then and the chaos is maximum, which probably aids the element of surprise in stealing.

It may be argued that Herring Gulls stay behind not because they are still hungry but because they loaf on the dump, while Lesser Black-backs when satisfied go home

to loaf. All available evidence does not favor this explanation. First, this study was made in the breeding season and the bulk of the data were collected when the gulls were feeding young. Second, if there were any loafers on the dump these consisted of both species.

Both species feed on the same things as judged by food remains in the colony and by direct observation on the dump. Apparently the different patterns of foraging behavior on the dump are not due to the evolutionary pressures for resource partitioning. Instead a system has developed in which the number of Lesser Black-backs on the Walney Island dump becomes largely dependent on the number of Herring Gulls. Herring Gulls appear better suited than Lesser Black-backs to feed on the dump itself because of their ability to dig. Lesser Black-backs are more agile than Herring Gulls and they take on the role of cleptoparasites. Intraspecific competition among cleptoparasitic Lesser Black-backs on the one hand, and efficient maximum exploitation of Herring Gulls on the other hand, are balanced to produce the preponderance of Herring Gulls seen feeding on this dump. The situation is somewhat analogous to a predator-prey system, i.e. for a given number of prey (Herring Gulls) only a certain number of predators (Lesser Black-backs) can exist.

## Acknowledgments

This paper is a contribution of the Animal Behaviour Research Group, Oxford University. The work was in part supported by a grant from the Natural Environmental Research Council to Professor N. Tinbergen, F.R.S. It is a pleasure to thank Prof. Tinbergen and Dr. Hans Kruuk for many helpful discussions, for reading the manuscript, and for companionship in the field. I thank Holker Estates Ltd. and the Lake District and Lancashire Naturalist Trusts for permission to work in the Walney gullery. Jerry Gallager, foreman on the dump helped me in many ways for which I am most grateful. Above all I thank Linda Verbeek, whose many sacrifices made the study possible. The paper has benefited from the comments of two anonymous referees.

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