The feeding behaviour of larus argentatus and other larus gulls at refuse tips

Greig, S. A.

THE FEEDING BEHAVIOUR OF

LARUS ARGENTATUS

AND OTHER *LARUS* GULLS

AT REFUSE TIPS

S.A. GREIG, B.A. (Cantab), M.Sc. (Dunelm)

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I certify that all material in this thesis which is not my own work has been identified and that no material is included for which a degree has previously been conferred upon me.

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CONTENTS

ABSTRACT

The feeding behaviour of wintering herring gulls, Larus argentatus, at refuse tips was investigated. Immature herring gulls were less successful than adults in independent foraging and in competitive interactions. They relied more heavily than adults on stealing and attacking to obtain food. Foraging ability improves over at least the first four years of life.

Three types of foraging at a refuse tip were distinguished: a) undisturbed primary feeding which was highly competitive, b) disturbed primary feeding in which gulls dipped for food from the air and therefore a high degree of manoeuvrability was required and c) secondary feeding which involved birds feeding at low densities on dispersed and partially covered refuse. Adult male herring gulls took part in more undisturbed feeding, where their greater size afforded them an advantage in competitive interactions, whereas females opted for more disturbed feeding, where they were advantaged by their smaller size and therefore lower wing loading.

The feeding methods used by the smaller numbers of great black-backed L. marinus and black-headed gulls, L. ridibundus present were also related to differences in competitive ability and manoeuvrability, both associated with body size. Use of kleptoparasitism increased with increasing body size. Both herring and great black-backed gulls preferentially attacked aggressive birds. Flock composition was variable such that when increased numbers of great black-backed gulls were present, there was also a shift towards the larger individuals of both species. This constituted an increase in the frequency of kleptoparasitic individuals and under these circumstances female herring gull feeding performance was depressed, whereas that of male herring gulls and of great black-backed gulls increased. Complex inter- and intra-specific interactions and the high degree of skill involved in feeding at a refuse tip led to large variation in the ability of individuals to exploit refuse as a food resource.

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GENERAL INTRODUCTION

"But resign this land at the end, resign it

To its true owner, the tough one, the sea-gull.

The palaver is finished."

from Landscapes: V. Cape Ann by T.S. Eliot

During this century there has been a progressive increase in the size of the breeding populations of several species of larid gull in both Europe and North America (Voous, 1960; Kadlec & Drury, 1968; Harris, 1970; Cramp *et al.*, 1974). The most marked increase has been in the number of herring gulls, *Larus argentatus*, with a 12-13% annual increase throughout the British Isles since the 1930s (Chabrzyk & Coulson, 1976). Seabirds are long-lived animals with life-cycles characterised by delayed maturity, low reproductive rates and a high degree of parental care of their offspring. These features are all typical of 'K-selected' species, which usually also have a stable population size maintained by density-dependent processes (Pianka, 1970). A rapid and sustained increase in numbers is therefore a rare occurrence in such an animal, and can be taken to mean that the factor or factors which were limiting the survival or birth rates of the animal have changed.

Bird populations may be regulated by predators, food supply, availability of nest sites (Lack, 1954) or by intrinsic social factors (Wynne-Edwards, 1962). Over the time scale of this century there has been no change in the number of available nest sites, and there is no reason to suppose a sudden change in some intrinsic factor responsible for self regulation. This leaves predation or food as possible candidates for the limiting factor which was relaxed at the beginning of this century, thus allowing the rapid expansion of gull populations since that time. The protective legislation which was introduced from 1869 onwards, together with more recent conservation measures, have resulted in a reduction in human exploitation of gull populations (Cramp et al., 1974). Nowadays the size of many gull colonies is such that it is difficult to imagine how egg-taking or shooting could have much effect on overall abundance, but when gull numbers were few, human predation may have been sufficient to control numbers. However the increase which has occurred could not have been sustained without sufficient food also being available.

Gulls are opportunist, generalist foragers and as such take a wide variety of foods. The food of gulls includes mussels and starfish, fish obtained by direct capture when shoals are near the surface and fish offal scavenged from fish quays and from fishing vessels at sea, earthworms, raw sewage and refuse (Hillis, 1973; Watson 1981; Mudge & Ferns, 1982; Sibly & McCleery, 1983a). As a result of the Public Health Act 1875 refuse began to be collected regularly and concentrated at relatively few disposal sites.

This, coupled with increases in the human population and a corresponding increase in the volume of refuse produced, has led to an increasing and more dependable food supply being provided at refuse tips. Such a concentrated food source could only be fully exploited by species, such as the gulls, which were accustomed to feeding in high density flocks at more natural food sources, such as fish shoaling near to the surface. Fish offal is another food used by gulls which has increased throughout this century, mainly through the intensification of commercial fishing. There is no evidence of major changes in the supply of any of the other foods which gulls take. In parallel therefore with the gull increase, there has been an increase in the availability of certain foods. Although the exact role of food availability in the increase in gull numbers is not known, both increased production of human waste and intensification of commercial fishing have been cited as major contributory factors (Harris, 1970).

A rapid and sustained increase is indicative of an unregulated population, but this cannot continue indefinitely as sooner or later some factor will become limiting. There is some evidence that herring gull populations have started to level off or even to decrease, since the mid 1960s in North America (Nisbet, 1978) and in S.W. Sweden (Kihlman & Larsson, 1974) and since the mid 1970s in the Bristol Channel area (Ferns, 1982). A recent B.T.O. survey of wintering gulls in Britain indicated that the rate of increase in wintering gull numbers had slowed in the last decade and that there had been a substantial 54% decline in the number of herring gulls compared with 1973 (Bowes *et al.*, 1984). The numbers of black-headed, *L. ridibundus*, common, *L. canus*, and lesser black-backed gulls, *L. fuscus*, had all continued to increase, whilst those of great black-backed gulls, *L. marinus*, showed a slight decline. Changes in winter distribution are probably especially important for lesser black-backed gulls, which have been wintering further north in recent years (Cramp & Simmons, 1983), but for the other species these trends are likely to be representative of changing population size. An increase in the incidence of botulism has been cited as a cause of increased herring gull mortality in some areas, but most evidence for this remains anecdotal (but see McDonald & Standring, 1978).

Whilst the early stages of the gull increase were characterised by local extension of the breeding range, there have also been large increases in colony size. It may be that increased competition near to these enlarged breeding colonies has led, in recent years, to food supply becoming limiting during the breeding season. This mechanism of food limiting seabird numbers in the breeding season was originally proposed by Ashmole (1963), in relation to tropical seabirds, but more recent work has suggested it may also apply to seabird colonies in higher latitudes (Gaston *et al.*, 1983; Furness & Birkhead, 1984). Mudge & Ferns (1982) reported intense local competition at refuse sites close to certain island herring gull and lesser black-backed gull colonies in the Bristol Channel and suggested that the lower growth rates of chicks at these colonies, compared with elsewhere, might be a consequence of this increase in competition for food. Sibly & McCleery (1983b) have gone so far as to suggest that herring gulls breeding at Walney in Cumbria would not be able to obtain sufficient food to breed without access to the local refuse tip, because of the limited temporal availability of other foods and the need for a breeding pair to adopt complementary feeding patterns during the incubation period. Although this clearly cannot apply to all gull colonies, since not all are near to refuse sites, it is indicative that obtaining sufficient food may present problems for gulls in the breeding season. Recent evidence from seasonal changes in weight and survival in the herring gull indicates that both are at a minimum during the breeding season (Coulson et al., 1983a) and this supports the theory that food may be limiting at this time. However the occurrence of mortality in the breeding season rather than in the winter may be due to the additional costs of breeding. How much food birds acquire during the winter and, as a direct consequence, the condition in which they enter the breeding season, may be critical for survival or reproductive success during that period.

Increased local concentrations of gulls do not only occur in the breeding season. Herring, great black-backed and black-headed gulls all undertake long distance movements in the winter months, from colder areas to warmer ones. Some herring gulls from northern Britain travel southwards down the east coast at the start of the winter and back again at the end to return to their breeding colonies (Coulson et al., 1983b). Herring gulls from northern Scandinavia travel to eastern Britain during the winter, forming a large proportion of the wintering herring gull population, particularly in the south east (Stanley et al., 1981; Coulson et al., 1984a). The great black-backed gulls which winter in north east England breed almost exclusively in Scandinavia (Coulson et al., 1984b) and the black-headed gulls which overwinter in north east England originate from countries bordering the Baltic (Horton et al., 1984). A consequence of these movements is that, during the winter months, the relatively small population of local breeding herring gulls in north east England is augmented by an influx of herring, great black-backed and black-headed gulls from elsewhere. This leads to increased competition between gulls at feeding sites in north east England during the winter.

Several studies have stressed the importance of refuse as a food for gulls especially during the winter months, when other foods are less available (Spaans, 1971; Kihlman & Larsson, 1974; Mudge & Ferns, 1982; Horton et al., 1983). However, although a refuse tip might appear to constitute a constant and superabundant food supply for gulls, several studies have indicated that this may not be the case. Gulls feed at high densities at tips and competitive interactions are frequent. Monaghan (1980) found that the proportion of immature herring gulls which fed at tips in the winter was much less than that expected from the average age composition of the herring gull population. She also found that female herring gulls fed more in the edge areas of the refuse pile, where competitive interactions were less frequent, and also that they tended to visit more feeding sites than did males. She suggested that both these facts were the result of the competitive nature of feeding at a refuse tip and that immatures and females were subordinate to males, and therefore at a disadvantage in competitive feeding. Sibly & McCleery (1983b), in a study of herring gulls during the breeding season, found that feeding efficiency, as measured by the rate of weight gain during a feeding trip, was less for females than for males when feeding at refuse tips, whereas there were no differences between the sexes at other feeding sites. They suggested that the females might be disadvantaged at tips by high levels of competition between birds. However they found no sex-related preferences for feeding sites. Age and experience may also be an important factor in tip feeding. Verbeek (1977a) found that immature herring gulls were less successful than adults in extracting edible items from the refuse, and that they attempted to supplement their food intake by stealing from adults. A further aspect of the foraging behaviour of gulls at tips which has received scant attention is the relationship between the feeding performance of the individual and the composition of the feeding flock. Other studies have shown that foraging in mixed species flocks can involve complex inter- and intra-specific interactions with implications for the comparative feeding success of members of the flock (Barnard et al., 1982).

Large numbers of herring gulls feed at refuse tips in north east England throughout the winter, together with smaller numbers of great black-backed and black-headed gulls. This thesis examines the nature of the feeding opportunities presented by a refuse tip and compares the ways in which these three gull species are able to exploit refuse as a food resource. The study's main emphasis is on the herring gull, this being the dominant gull species which feeds at refuse tips in this area. Over 9000 herring gulls have been caught at refuse tips in the Durham area, measured and each given a unique combination of coloured plastic leg rings, as part of a study of the ecology of wintering herring gulls. Both the sex and race of each herring gull can be identified from its biometrics and from differences in mantle shade (Coulson et al., 1984a). The existence of a large number of uniquely marked animals allowed individual variation in feeding methods and performance to be studied.

The thesis is presented as four papers. The first paper deals with age-related differences in foraging success in herring gulls and examines the ways in which young birds acquire feeding skills. The second paper looks at the foraging strategies of adult male and female herring gulls and considers how these strategies relate to differences in competitive ability and manoeuvrability, both associated with body size. The third paper considers the comparative feeding ecology of herring, great black-backed and black-headed gulls, and includes a comparison of the British and Scandinavian races of herring gull. The fourth paper looks in more detail at kleptoparasitic behaviour in great black-backed and herring gulls, the decision rules involved and the implications of changes in flock composition for the comparative foraging success of individuals of the two species and of different age, sex and race in the case of the herring gull.

2. AGE RELATED DIFFERENCES IN FORAGING SUCCESS IN THE HERRING GULL

2.1 Introduction

In higher animals, particularly those which are long-lived, there are many skills necessary for survival which require a period of learning before they become fully effective (Johnston 1982). Some skills are learned relatively quickly, for example most birds are able to fly at only a few weeks of age. There is evidence that efficient foraging, involving as it does a wide variety of skills, may take considerably longer to develop. Lower foraging ability in immatures compared with adults has been demonstrated in a number of seabird species (Orians 1969; Recher & Recher 1969; Dunn 1972; Buckley & Buckley 1974; Barash et al. 1975; Verbeek 1977a,b; Ingolfsson & Estrella 1978; Morrison et al. 1978; Searcy 1978). With the exception of Verbeek (1977a), these involved studies of a single foraging skill with no interaction or competition between individuals. In the majority of cases only two age groups were compared.

The herring gull Larus argentatus is an opportunistic, general feeder and therefore makes use of a wide range of foraging skills. The majority of herring gulls do not breed until the fifth year of life (Chabrzyk & Coulson 1976) and in large colonies many do not breed until they are six years old (Coulson, et al. 1982). Birds in their first, second, third and fourth years of life birds are distinguishable on the basis of plumage characteristics. The plumage of many immature birds of known age which we have examined has shown that this is a reliable method of determining their age and that exceptions are infrequent. It is therefore possible to investigate the development of foraging skills under field conditions over the first four years of life and to compare these performances with that of adults. The data were collected at refuse tips in N.E. England throughout the winter, at which time refuse is a frequently used food source for the herring gull (Spaans 1971; Kihlman & Larsson 1974; Mudge & Ferns 1982). Feeding occurs in mixed flocks of immature and adult birds and so in this study the foraging ability of birds of different ages could be measured in the same situation. Further, it was also possible to study the effect of social interactions on individual foraging success.

2.2 Methods

Data were collected on feeding behaviour of herring gulls using colour video recordings made at four refuse tips between October 1981 and February 1982. Approximately half of the refuse is of household origin, and the distribution of edible items within it is clumped. The refuse is delivered throughout the day and a bulldozer works almost continuously compacting the rubbish and then covering it with earth. Typically, gulls fed briefly whilst the bulldozer was working, but the only feeding period of any length was from 1200-1230 hours when the tipping and bulldozing ceased. All recordings were concentrated on the area where most of the gulls were feeding. In every case the birds were feeding either on freshly dumped refuse or refuse which had been recently bulldozed into position but not covered with earth.

Data were recorded from immature birds aged by plumage characteristics and from individually colour-ringed immatures and adults. Throughout this paper birds in their first, second, third and fourth year of life are referred to as first, second, third and fourth year birds respectively. The term immature is used to refer to all these four age groups considered together. The feeding birds were usually at a high density of 5-10 birds/m and, on average, a selected individual usually moves out of view within 75-100 s. Observation periods of 15-s units were used and the following data were recorded for each bird in a 15-s unit; a) number of pecks, b) number of swallows (each defined as a food item being taken and swallowed), c) number of paces ranked in one of four categories, 0 - none; 1 - less than 5; 2 - 5-10; 3 - over 10, d) number and nature of encounters with other birds including the age of the other gulls, whether the subject initiated the attack or was the recipient, which of the birds was feeding at the time of the encounter, the outcome of the encounter. Detailed recording of encounters was restricted to those which involved the subject and one to three other birds. Cases involving larger groups of birds formed only 1% of the total interactions.

Two types of encounter were distinguished; i) a attack made in order to gain food by the displacement of another bird and ii) an attack made in order to drive away a bird intruding on to the subject's feeding patch, i.e. an territorial attack in defence of food. In this second type of encounter the intruder typically adopted a hunched, submissive posture close to a feeding bird and, after remaining there for some time, approached closer and attempted to steal food from the patch that the feeding bird was using. Such attempts almost invariably resulted in an attack by the feeding bird.

Success in a displacement attack was defined as the displacement of the opponent from its position (which was then taken up by the attacking bird). Success in an attack in defence of food was characterised by the retreat of the intruder (the attacking bird remaining in possession of the food).

Feeding rate is measured by the number of swallows achieved in 15 seconds. Feeding efficiency is the proportion of pecks which resulted in swallows.

Data were recorded from a total of 171 individuals, for a total of 985 15-s units. This represents the analysis of 140 min. of feeding activity observed on 19 days.

2.3 Results

2.3.1 Feeding rate

Feeding rate increased with age (Fig.2. 1). First, second and third year birds all had significantly lower feeding rates than adults (Mann Whitney U test, $P < 0.001$, < 0.05 and < 0.05 respectively). By the time birds reach the fourth year of life, the estimate of their feeding rate was not significantly lower than that of adults.

Feeding efficiency also increased with age and followed the same pattern as feeding rate (Fig 2.2). First and second year birds both showed significantly lower feeding efficiency than adults (χ^2_1 = 17.78, 4.50, $P < 0.001$, $P < 0.05$ respectively). There were no significant differences between birds in their third year and older although the trend of increasing feeding efficiency continues until the fourth year of life. In order to establish the ways in which immature birds were less efficient, three components of foraging were investigated; i) peck rate, ii) walking rate, iii) the rate, nature and outcome of encounters between birds.

2.3.2 Peck rate

There is no progressive increase in peck rate with age in immature birds (Table 2.1). Although adults have a higher peck rate than all age classes of immature birds the difference is small and in no case is it significant. One possible explanation for the small difference in peck rate which is observed is that adults turn objects over in search

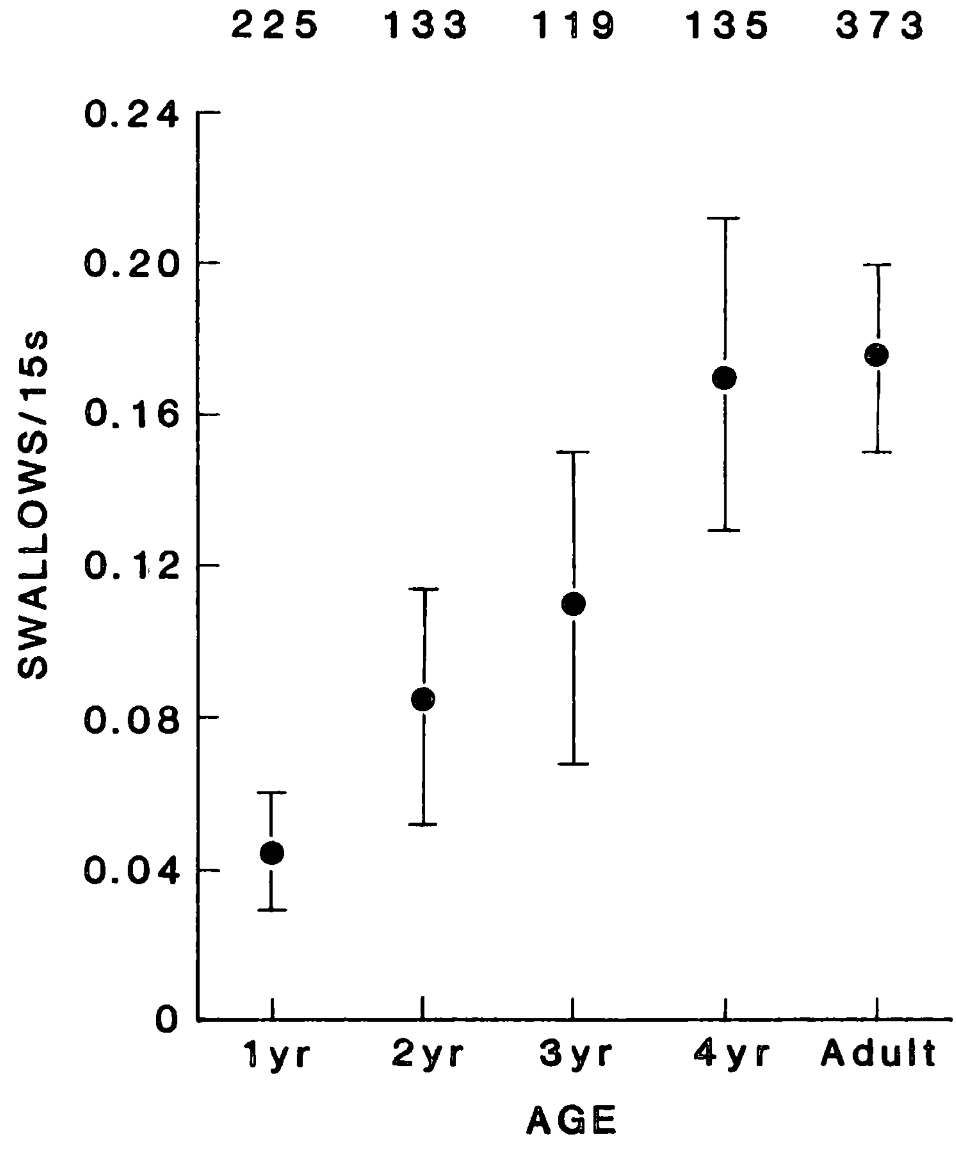

Fig. 2.1 Mean feeding rates ± 1 SE for different aged herring gulls. Sample sizes are shown above each point. The average age of an adult is 9 years calculated on the basis of adult survival of 93.5% and an average population rate of increase of 13% per annum (Chabrzyk & Coulson 1976).

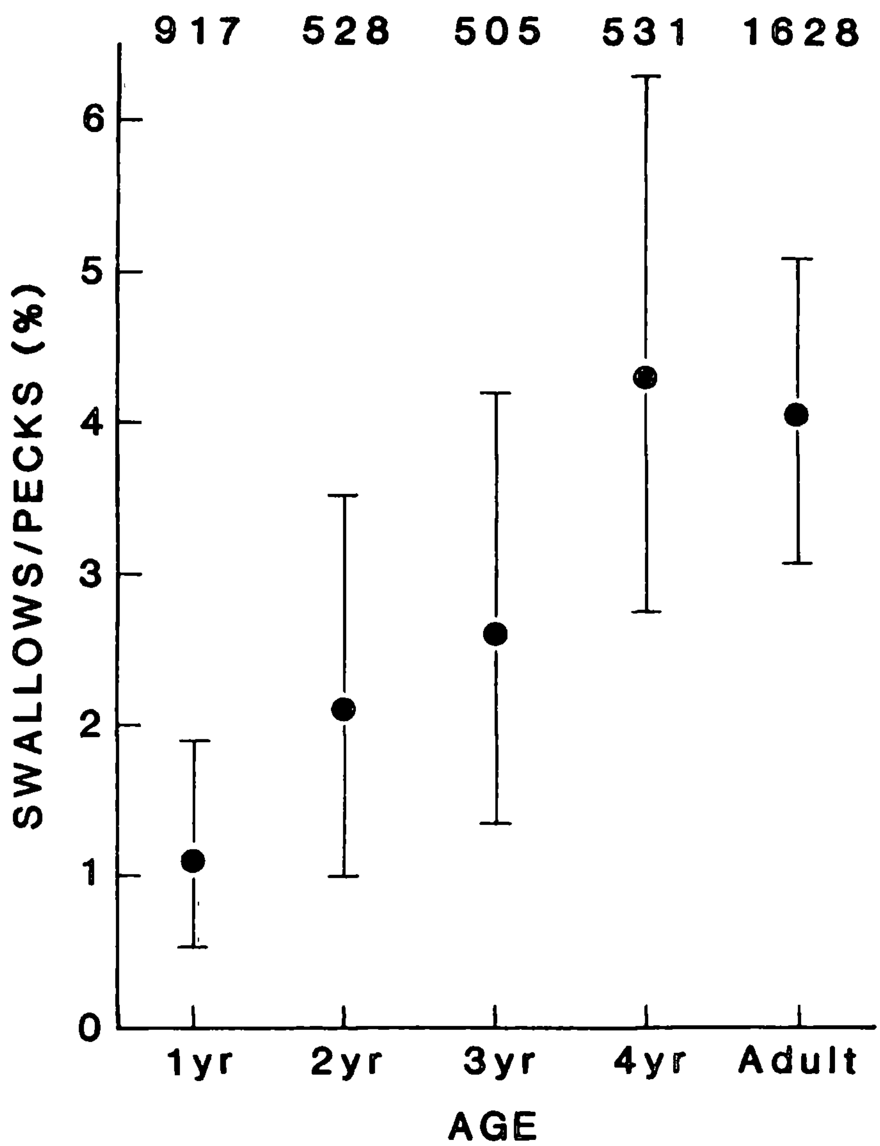

Fig. 2.2 The percentage of the total number of pecks which are successful (i.e. result in a food item being swallowed) for herring gulls of different ages, with 95% confidence limits calculated using an Arcsin transformation. Sample sizes are shown above each point.

Table 2.1 Mean Peck Rates for Herring Gulls of Different Ages

Age class	No. of samples	Mean no. pecks/15 s	S D
1st yr.	225	4.08	2.86
2nd yr.	133	3.97	2.81
3rd yr.	119	4.24	2.88
4th yr.	135	3.93	2.63
Adult	373	4.37	2.61

Table 2.2 The Number of Paces/ 15 s Taken by Two Age Classes of Herring Gulls whilst Feeding Together on Refuse Dumps

Age class		Number of Paces/15 s				
		0	1-4	5-10	<10	Total
1st & 2nd yr.	No.	0	115	157	86	358
	%	0	32	44	24	
over 2 yrs.	No.	6	238	288	95	627
	%	1	38	46	15	

Note: After combining the none and 1-4 paces/15 s categories, the distributions of records of paces for the two age classes are significantly different (χ^2_2 = 12.25, $p < 0.01$).

of edible items at a faster rate than do immature birds (Verbeek 1977a). Although adults do not peck a great deal faster than immatures, their pecking is more productive and uncovers more food items per unit time.

2.3.3 Walking rate

There is no significant difference between the mean or the distribution of values for walking rate of third and fourth year birds and adults, and these age categories have been grouped together. This older age group has an approximately 13% lower walking rate than first and second years (Table 2.2). This difference is statistically significant ($P < 0.01$). On average first and second years take 133 paces per food item swallowed compared to the 41 paces per swallow of older birds.

2.3.4 Encounter rates

Owing to large variances in encounter rate and the smaller sample sizes for second, third and fourth year birds, no significant differences can be shown between these age groups and the data for these age classes have been combined. The proportions of adult and immature birds being involved in an encounter in a 15-s unit are shown in Table 2.3. Immature birds are significantly more likely to be involved in an encounter in 15 seconds than are adult birds ($\chi^2_1 = 9.08$, $P < 0.01$). There are two ways of looking at an encounter; (i) from the point of view of the attacking bird; (ii) from the point of view of the attacked bird. The rates at which different aged birds attack and are attacked are

Table 2.3 Probabilities of being Involved in an Encounter in 15 s for Herring Gulls of Different Ages

Age class of subject	No. of samples	*All encounters	Encounter in which subject attacked	Encounter in which subject was attacked
1st yr.	225	0.182	0.120	0.067
2nd-4th yr.	387	0.191	0.106	0.090
Adult	373	0.115	0.056	0.064

*Because occasionally a bird attacked and was attacked within the same 15-second observation unit, the value in this column may be less than the sum of the values in the last two columns.

considered separately.

Attack rates. Immature birds are significantly more likely to make an attack in 15 s than are adult birds (Table 2.3, χ^2_1 = 8.47, P < 0.01). There is no signficant difference in the proportions of attacks of different types made by different aged birds. Considering all age groups together, 59% (N = 189) of attacks were made in order to obtain food by the displacement of an actively feeding bird (displacement attacks), the remainder being attacks to drive away intruders (attacks in defence of food). The proportion of birds making a displacement attack in 15 s decreases with age (Fig. 2.3). The displacement attack rate of birds in their first year is twice that of adults (χ^2_1 = 4.99, P < 0.05) with the 2-4 year age class being intermediate. There is no corresponding age-related trend in attacks in defence of a food area (Fig.2.4). Since this type of attack is precipitated by the intrusion of a bird into the attacker's feeding patch, it is a function of the intruder's behaviour rather than that of the attacking bird. It is therefore more appropriate to look at the age of intruders and this is described in the following section.

Rates of being attacked. The proportion of immature birds which are attacked in 15 s is not significantly different from that of adults (Table 2.3). However the reason for attacks does vary according to the age of the attacked bird. Figure 2.5 shows that first years are less likely to be

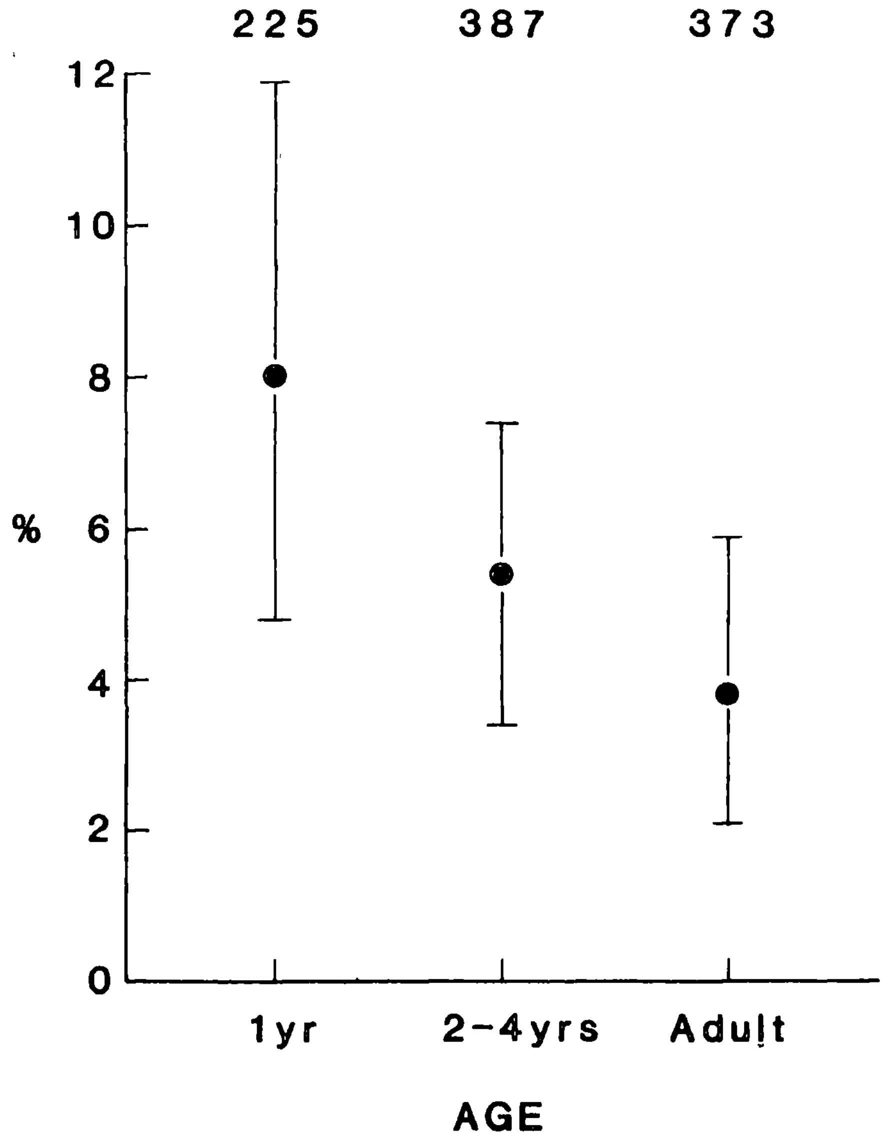

Fig. 2.3 The percentage of herring gulls which make a displacement attack in 15 s for birds of different ages, with 95% confidence limits calculated using an Arcsin transformation. Sample sizes are shown above each point.

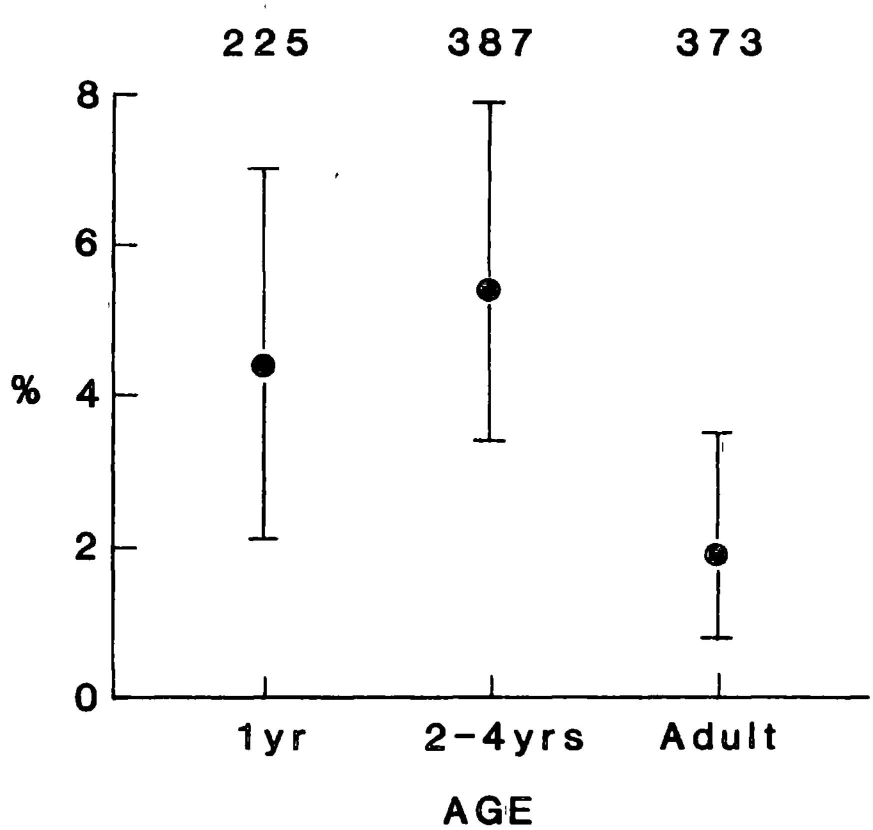

Fig. 2.4 The percentage of herring gulls which attack in defence of food in 15 s for birds of different ages, with 95% confidence limits calculated using an Arcsin transformation. Sample sizes are shown above each point.

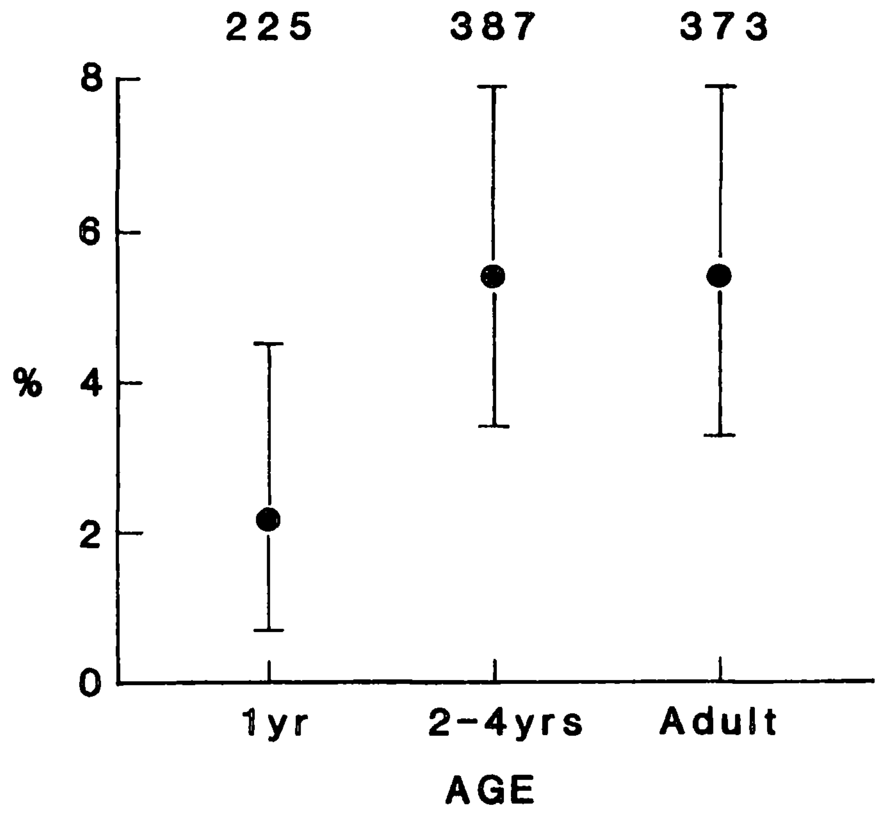

Fig. 2.5 The percentage of herring gulls which are subject to a displacement attack in 15 s for birds of different ages, with 95% confidence limits calculated using an Arcsin transformation. Sample sizes are shown above each point.

subject to displacement attacks than are older birds (first year compared with older birds; $\chi^2_1 = 3.72$, $P < 0.05$). This is not surprising since displacement attacks are directed at feeding birds and fewer of these are first years due to their lower feeding rates. In contrast, Fig 2.6 shows that immature birds are significantly more likely to be attacked by birds defending food (immatures compared with adults; $\chi^2_1 = 7.36$, $P < 0.01$). Since all major intrusions result in an attack by the feeding bird, the rate of being attacked by birds defending food can be equated with the rate of intruding. First year birds are 5 times more likely to intrude on to the feeding patches of others than are adults, with the 2-4 year age class being intermediate.

2.3.5 Outcome of encounters

The proportions of attacks in which different aged birds are successful are given in Table 2.4. In 89% of encounters (N = 189) the bird which initiated the attack won, irrespective of its age, the other bird giving way immediately. Considering all age groups together birds are significantly more likely to win an attack in defence of food than a displacement attack ($\chi^2_1 = 7.9$, $P < 0.01$). Only two successful intrusions were observed, i.e. in which the feeding bird withdrew, and these were both adults intruding onto the feeding area of immature birds. In neither case did the intruder gain any food. Thus, intrusion onto another bird's feeding patch is a most unsuccessful method of obtaining food.

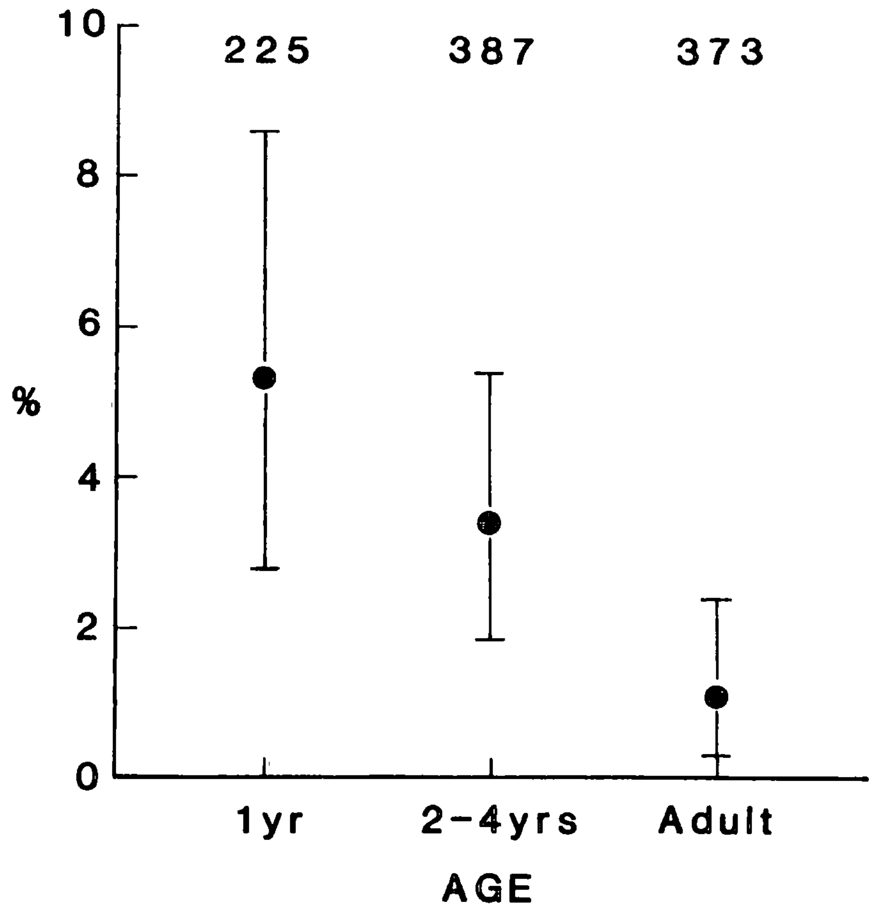

Fig. 2.6 The percentage of herring gulls which intrude on to another's feeding patch in 15 s for birds of different ages with 95% confidence limits calculated using an Arcsin transformation. Sample sizes are shown above each point.

Table 2.4 Proportions of Attacks which are Won by Herring Gulls of Different Ages (sample sizes shown in Parentheses)

Age class of Attacker	All Attacks	Displacement Attacks	Attacks in Defence of Food
1st yr.	0.83 (42)	0.73 (28)	0.93 (14)
2nd yr.	0.86 (15)	0.83 (12)	1.00 (3)
3rd yr.	0.90 (20)	0.91 (11)	0.90 (9)
4th yr.	1.00 (26)	1.00 (10)	1.00 (16)
Adult	0.91 (86)	0.84 (51)	1.00 (35)
All ages	0.89 (189)	0.85 (112)	0.97 (77)

Success in a displacement attack is not necessarily directly linked to food gain. Displacement attacks by adults result in 60% (N = 15) of the attacking birds swallowing food within 15 s. The corresponding figure for attacking immature birds is significantly lower at 15% (N = 46, χ^2_1 = 9.52, P < 0.01). Thus, despite approximately equal success in displacing birds, adults benefit considerably more from each displacement attack than do immature birds, due to the adult bird's greater ability to detect and extract edible items from the refuse pile. However only 11% (N = 155) of food items swallowed by birds of over 1 year old are gained as a result of a displacement attack whereas the corresponding figure for first year birds is 33% (N = 24). This difference is significant (χ^2_1 = 6.89, P < 0.01). This suggests that first year birds rely more on obtaining food from other birds through displacement attacks whereas older birds gain almost all their food by searching the refuse pile itself.

2.4 Discussion

Under the feeding conditions investigated immature herring gulls had a lower peck rate and took more paces per unit time than adult birds. They made more attempts to gain food from other birds, by displacement attacks and by intrusions on to the feeding patches of others, rather than searching the refuse itself. The evidence from displacement attacks suggests that first year birds in particular were more dependent than older birds on other gulls for the location of food. Although immature gulls were as successful as adults in displacing birds, they were less able to obtain food from their newly acquired feeding patch. When immature birds intruded on to the feeding patches of others, they were invariably attacked, driven off and obtained no food. Thus immature birds were considerably less skillful than adults both in finding and obtaining food from refuse. This lack of skill and greater dependence of immature herring gulls on other birds for obtaining food is also described by Verbeek (1977a,b). He found that immature herring gulls feeding on refuse and on starfish were less skilful than adults and used chasing and stealing as an important method of obtaining food.

In all aspects of foraging examined in this study first year and adult birds formed the two extremes with second, third and fourth year birds being intermediate. Therefore the foraging success of herring gulls at refuse sites gradually improves over at least the first four years of life. Several skills are required in order to feed successfully in such a situation. The bird must be able to find and to recognise edible items and to extract them from the refuse. Feeding is highly competitive since the gulls are at high density and the time available for feeding is limited. It must, therefore, be able to obtain food rapidly before the edible fraction of the refuse becomes depleted by the other feeding gulls. Whilst trial and error learning is undoubtedly of considerable importance, close contact and interactions with adults, which have mastered the ability of feeding rapidly and successfully at refuse sites, may assist immature birds to learn and improve foraging skills. The enhancing effect of social learning on feeding efficiency has been observed in a number of bird species (Hinde & Fisher 1951; Lockie 1956; Klopfer 1959; Murton et al. 1971; Krebs et al. 1972).

When feeding at a refuse site, immature herring gulls expend more energy per unit time than adults both because of their higher encounter rates and higher walking rates. In addition, immature birds have lower feeding rates. Therefore, in terms of food gain per unit of energy expended, the foraging of immature birds is considerably less efficient than that of adults. However, survival and body weight are at a maximum for all ages of herring gulls during the winter months (Coulson et al. 1983a). This suggests that most immature birds are able to gather sufficient food for survival, albeit less efficiently than adults. The lower feeding efficiency of immature birds has several implications. One is that they have to feed for longer and, possibly in sub-optimal areas of the refuse tip, in order to obtain sufficient food (Davis 1975; Monaghan 1980). Another implication is related to the timing of first breeding. Most seabirds do not breed until they are 3 years old and this delay in breeding has often been linked to the need to master foraging techniques and to learn foraging areas (Lack 1968). A breeding bird must feed itself, its offspring and sometimes, its mate. In addition the time available for foraging is decreased since time is also required for courtship, site-retention and other reproductive activities. The age of first breeding must therefore be closely linked to the attainment of a certain threshold in feeding efficiency. In the herring gull breeding is delayed until the fourth or fifth year of life or later and the first attempt at breeding is often unsuccessful (Chabrzyk & Coulson 1976; Coulson et al. 1982). Low success in birds breeding for the first time is widespread in seabirds (Ryder 1980). This study suggests that for at least the first four years of life, and possibly for longer, the feeding efficiency of a herring gull increases as foraging techniques are learnt and perfected. The delay in first breeding in the herring gull may be a consequence of the long period of experience required before foraging skills are fully mastered.

Herring gulls are general and opportunistic feeders and, as such, they use a wide variety of feeding sites, each requiring different foraging techniques. Whether immature birds are less skillful at other feeding sites, and if so, what period of experience is necessary before they are fully efficient, remain to be investigated.

3. FEEDING STRATEGIES OF MALE AND FEMALE ADULT HERRING GULLS

3.1 Introduction

Whatever the ultimate factors involved in the evolution of sexual dimorphism, one consequence may be some degree of niche separation. Morphological differences between males and females can affect the costs and benefits of different foraging strategies and may result in the establishment of differences in various aspects of foraging behaviour. For example, in two species of woodpeckers, SELANDER (1966), related the degree of sexual dimorphism in bill size and shape to the extent to which the two sexes foraged differently. SMITH & EVANS (1973) showed that in Bar-tailed Godwits (<u>Limosa lapponica</u>) feeding on mudflats, females fed beyond the tideline more than males and were able to use their longer beaks to reach deeper prey.

The degree of sexual dimorphism is variable from species to species. In some cases, one sex may be twice the size of the other e.g. some mustelids and some birds of prey (ERLINGE, 1979; NEWTON & MARQUISS, 1982), whereas in others the differences are only slight. In the herring gull (<u>Larus argentatus</u>), adult males are on average larger than adult females. Although the degree of sexual dimorphism is relatively small, (females being on average 83% of male weight), the sexes can be separated on the basis of body measurements with only 5% misidentification (COULSON <u>et al</u>., 1983c). Herring gulls feed in mixed sex flocks at a variety of feeding sites. In a study of herring gulls during the four week incubation period, SIBLY & McCLEERY (1983b) found individual differences in food preferences and in foraging efficiency at different sites. Refuse tips were the only site where a difference in feeding efficiency between the sexes was demonstrated, with females being less efficient than males. They suggested that the competitive nature of feeding at a refuse site contributed to the lower efficiency of females. In a number of species, sex-related differences in feeding behaviour have been attributed to superior competitive ability of males (e.g. Cercopithecus monkeys; GAUTIER-HION, 1980, HARRISON, 1983; three-toed woodpeckers, Picoides tridactylus, HOGSTAD, 1976). In these cases, social dominance may constitute a behavioural means by which intra-specific competition and costly interactions are reduced, albeit at the expense of subordinate individuals (i.e. females), who are forced to feed less efficiently or to move to another feeding site. However, COULSON et al. (1983c) have shown that in the winter months (October-February), the sex ratio of herring gulls at tips is increasingly biased towards females. This female biased sex ratio suggests that females use tips more than males during the winter months.

The aims of the present study were (i) to examine the foraging opportunities presented at a refuse site; (ii) to investigate the foraging techniques used by adult male and female herring gulls at refuse tips during the winter months; (iii) to assess the importance of social dominance in determining the relative foraging performances of males and females.

3.2 Methods

(a) Use of refuse tips by adult male and female herring gulls

In order to compare the use made of refuse tips by adult male and female herring gulls, direct observations were made at Tow Law refuse tip, Co. Durham, between October 1982 and February 1983. This tip was chosen for this part of the study because most of the area, including both feeding and loafing sites, could be scanned from a single vantage point. Data were recorded from individually colour-ringed adults. These birds had been sexed by the head and bill length (COULSON *et al.*, 1983c). A total of 13 complete daylight-hour observations (85 hours in all) were made at this refuse tip. On each day, the times of arrival and departure of individually marked adult herring gulls were recorded using searches at 15 min intervals. Feeding bouts at the refuse tip were divided into three types.

1. Undisturbed primary feeding: This involved undisturbed feeding on freshly dumped rubbish which had not been covered with earth. The main opportunity for this type of feeding was at lunchtime (1200-1230 BST) when bulldozing stopped and it was characterised by a high density of birds.

2. Disturbed primary feeding: This involved feeding whilst a bulldozer was working. It also involved a high density of birds and was chaotic, with each herring gull settling on the ground for less than 10s at a time.

3. Secondary feeding: This involved feeding on rubbish which had been covered with earth. The gulls were at low density and feeding of this type occurred at the beginning and at the end of the day.

The number and types of feeding bouts, in which individually marked gulls participated, were recorded by direct observation. These data, and information on arrival and departure times, were collected on a total of 74 marked adult male herring gulls and 85 marked adult female herring gulls.

(b) Foraging behaviour of adult male and female herring gulls

In order to examine foraging methods and to compare foraging efficiency between the sexes, colour video recordings were made of sexed and colour-ringed herring gulls, feeding at five refuse sites, namely Coxhoe, Wingate, Hett Hills, Consett and Tow Law, Co. Durham. These recordings were made between October 1981 and February 1982 and October 1982 and February 1983. The recordings were almost entirely confined to undisturbed primary feeding. It was difficult to obtain detailed feeding behaviour on sexed individuals during disturbed primary feeding, since, in the general scramble, it was not possible both to read the colour combination and then to follow an individual, recording its feeding activity, for more than a few seconds. Secondary feeding involved only small numbers of herring gulls and little data on the feeding behaviour of sexed individuals was collected during such feeding.

During undisturbed primary feeding, the gulls were at a density of 5-10 birds per m^2 and each selected individual moved out of view within, on average, 75 seconds. Therefore an observation unit of 15 seconds was used in the analysis of video recordings, and the following data were collected for each individually marked bird, in each unit: (a) number of pecks; (b) number of food items swallowed; (c) number of paces ranked in one of four categories: 0: none;1: one to four;2: 5-10;3:over 10; (d) number and nature of encounters with other birds. A total of 650 minutes of feeding activity was filmed on 42 days and feeding behaviour data were recorded from 52 adult male herring gulls and 67 adult female herring gulls for a total of 803 15-s observation units. These data were also collected on a smaller random sample of unsexed adult herring gulls, during both disturbed primary feeding and secondary feeding, so that feeding and encounter rates in different feeding situations could be compared.

(c) Statistical methods

Behavioural data were analysed using parametric rather than non-parametric statistics because of the need to take account of individual variation; the data were transformed where appropriate. Analysis of variance was used to test the significance of differences between individuals within each sex. Where there was no significant individual variation, all observations were pooled. Where there was significant variation between individuals, the assumption of independence between observations was invalid. The problem was overcome by use of the random effects model of analysis of variance (SNEDECOR & COCHRAN, 1967). The estimated variance of the sample mean, $\underline{S}^2$, was modified for the case of unequal sample sizes according to the formula;

$$S^2 = \frac{1}{N} \left(\hat{\sigma}^2 + \frac{\sum_{i=1}^{a} n_i^2 \; \hat{\sigma}_A^2}{N} \right)$$

where $\hat{\sigma}_A^2$ is the estimate of the component of variance, $\hat{\sigma}^2$ is the estimate of the random error attached to each observation, N is the total number of observations, $\underline{n}_i$ is the number of observations of an individual and $\underline{a}$ is the number of individuals (Dr. P. Green, pers. comm.). In this way, the variance of the sample mean was adjusted to allow for individual variation. Both swallowing a food item and having an encounter with another individual were rare events, scoring a high proportion of zeros in each observation period. A square root transformation to $\sqrt{X+1}$ was used to stabilize the variance (SNEDECOR & COCHRAN 1967). Statistical tests were then performed on the transformed data. Means and 95% confidence limits in the square root scale were then reconverted to the original scale by squaring and subtracting one.

(d) Sexual dimorphism in herring gulls

On average, the adult male herring gull is 20% heavier, has a 10% longer and deeper bill and a 5% longer wing than the female (based on samples of 261 males and 219 females). Although seasonal weight changes are known to occur, COULSON et al. (1983a) found that the pattern and proportion of weight change was the same in both sexes, with male and female weight reaching a peak in mid-winter. Head and bill length remained constant from fledging, but bill depth continued to grow throughout the life of the bird. (COULSON et al. 1981). Whilst bill depth alone cannot be used to accurately age individuals, comparison of the mean bill depth, between groups of herring gulls of the same sex, gives a measure of differences in the mean age between groups. In this study, comparisons of the mean bill depth of the colour-ringed male and female herring gulls present at the tip have been used to indicate changes in the age composition.

3.3 Results

3.3.1 Use of refuse tips by adult male and female herring gulls.

At Tow Law refuse tip, no significant differences were found in the average time of arrival, departure or length of stay each day between male and female herring gulls. The length of stay at the tip varied from 15 mins to 345 mins, with a mean of 110 mins. This is a minimum value since it is based on the first and last sighting of each marked individual on the tip area. For much of the day, large numbers of gulls were present either loafing or searching for worms in fields close to the tip, and it is likely that the majority of herring gulls were either on the tip or nearby for much of the daylight period.

Although a refuse tip might appear to constitute a source of readily available, superabundant food, this was not the case. For much of the day, the gulls were inhibited from feeding by the high level of disturbance created by both vehicles and people moving around on the tip. This was reflected in the time gulls spent feeding at the tip (Fig. 3.1). For both males and females, the mean never exceeded 55 mins per day and had a mean value of 30 mins, although the working day at the tip lasted between 7 and 8 daylight hours. There were no consistent differences between males and females in the time spent feeding each day. Both sexes showed a trend of increasing feeding time as the season progressed, although this was significant only for males (Fig. 3.1). The mean bill depth of marked males tended to decrease seasonally, with no corresponding trend in head and bill length (Fig. 3.2). This suggests that the male herring gulls present in January and February were, on average, younger than those present in October and November. There

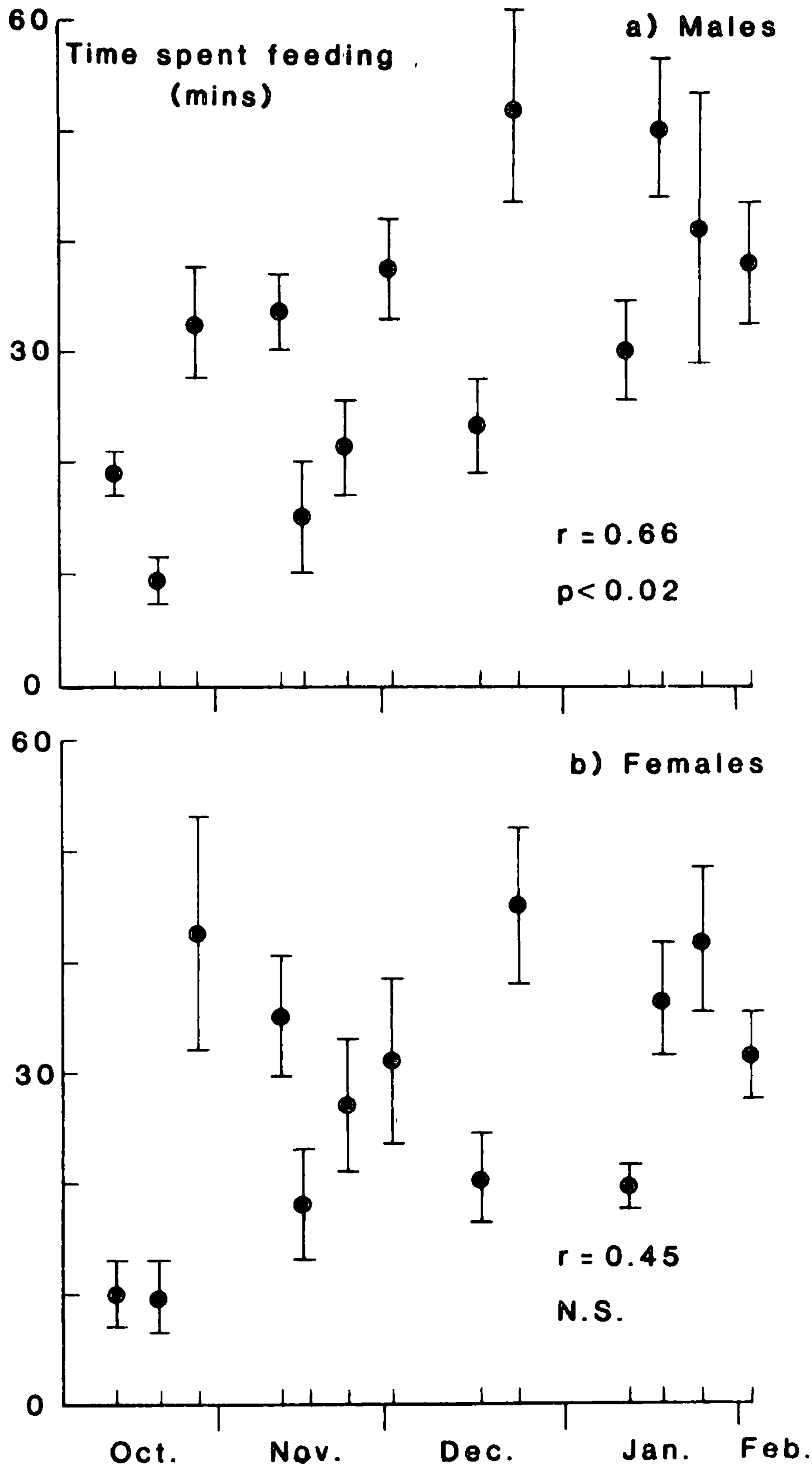

Fig. 3.1 Time spent feeding each day by a) male and b) female adult herring gulls at Tow Law refuse tip throughout the winter. (means ± 1 SE)

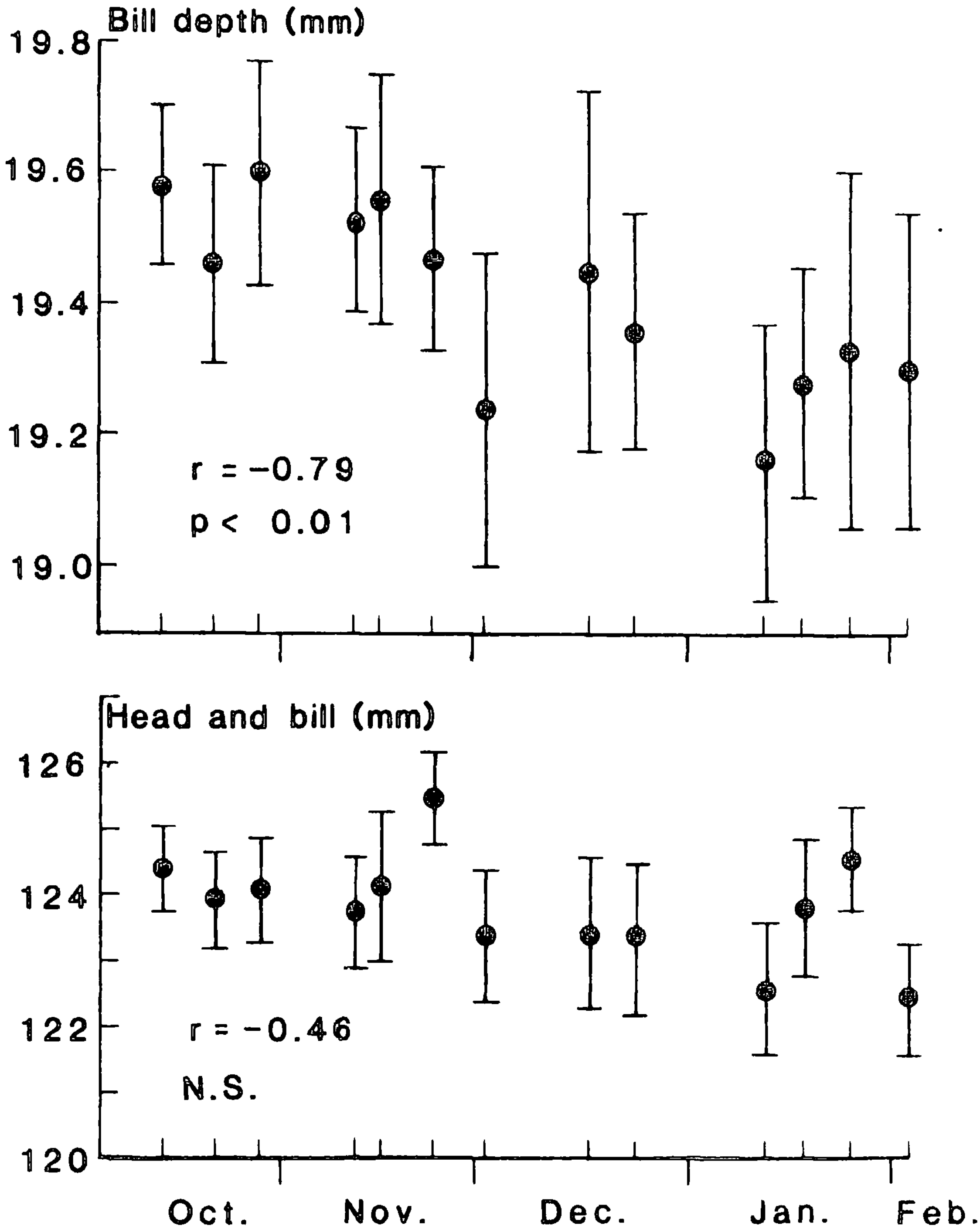

Fig. 3.2 Biometrics of male adult herring gulls present at Tow Law refuse tip throughout the winter.
(means ± 1 SE)

were no similar seasonal trends in females.

3.3.2 Type of feeding

Table 3.1 summarises the main characteristics of the three types of feeding recorded at Tow Law refuse tip. On average, primary feeding, both disturbed and undisturbed, involved four times more herring gulls (and nine times more adult herring gulls) than secondary feeding (Table 3.1). Both types of primary feeding were comparable in terms of swallowing rate, whilst secondary feeding offered a significantly lower food return. The encounter rate, which gives a measure of the level of competitive interactions between birds, was considerably higher in undisturbed primary feeding than in disturbed primary or secondary feeding (Table 3.1). During disturbed feeding, the birds did not settle on the ground for long enough to interact with each other and during secondary feeding, the density of feeding birds was so low that interactions were very infrequent. Undisturbed primary feeding was therefore highly competitive, the herring gulls both attacking for, and defending, good feeding patches.

The extent to which adult male and female herring gulls used their feeding opportunities differently is shown in Table 3.2. Overall, proportionally more males than females participated in undisturbed primary feeding, whilst proportionally more females than males participated in disturbed primary feeding. The difference between males and

Table 3.1 Comparisons of the characteristics of undisturbed primary, disturbed primary and secondary feeding.

Feeding type	Mean number of herring gulls	% immature herring gulls	Mean daily duration (mins)	Mean duration of feeding bout (mins)	Mean swallowing rate (swallows/15s) for random sample of adult herring gulls	Mean encounter rate (encounters/15s) for random sample of adult herring gulls
1. Undisturbed primary	110 ± 26	27	79.5 ± 24	15.6 ± 7.2	0.17 (0.12–0.22)	0.16 (0.13–0.19)
2. Disturbed primary	90 ± 14	27	21.6 ± 7	6.5 ± 1.4	0.27 (0.07–0.49)	0.02 (0–0.06)
3. Secondary	26 ± 7	75	52.5 ± 19	20.7 ± 5.5	0.03 (0–0.10)	0.03 (0–0.10)

(All means given with 95% confidence limits.)

Differences in swallowing rate and encounter rate between feeding types (Student's 't' tests on transformed data).

	Swallowing rate	Encounter rate
Undisturbed primary vs. disturbed primary	$t = 0.95$, N.S.	$t = 5.62$, $p<0.001$
Undisturbed primary vs. secondary	$t = 3.27$, $p<0.01$	$t = 3.42$, $p<0.002$
Disturbed primary vs. secondary	$t = 2.26$, $p<0.05$	$t = 0.36$, N.S.

Table 3.2 The proportion of herring gulls using three methods of feeding during a day. The values are based on colour-ringed male and female adults and the results are divided into two time periods of the winter, 7 days of observation being combined in the first and 6 days in the second. The percentages for each sex do not sum to 100 since some individuals took part in more than one type of feeding on one day.

Feeding type	Time period	No. of males feeding	% using this method	No. of females feeding	% using this method	Significance[1])
Undisturbed primary	Oct. 13-Dec.15	91	76	61	59	d = 1.99 $p < 0.05$
	Dec. 16-Feb. 3	62	92	103	83	d = 1.70 N.S.
Disturbed primary	Oct. 13-Dec.15	91	40	61	61	d = 2.74 $p < 0.01$
	Dec. 16-Feb. 3	62	39	103	48	d = 1.21 N.S.
Secondary	Oct. 13-Dec.15	91	30	61	31	d = 0.78 N.S.
	Dec. 16-Feb. 3	62	24	103	26	d = 0.19 N.S.

[1]) Differences between the proportions of each sex participating in each type of feeding were tested by combining the 2x2 tables for each day according to the method described by SNEDECOR & COCHRAN (1967).

females, for both types of primary feeding, were most marked in the first half of the winter period, (i.e. October-mid December), there being no significant differences between the sexes in the latter half of the winter (Table 3.2). Both sexes showed a seasonal increase in the proportion of birds participating in undisturbed primary feeding, the trend being most marked in females (χ^2 test for linear trend in proportions: females; χ^2_1 = 19.31, $p < 0.001$: males, χ^2_1 = 7.49, $p < 0.01$). Since both types of primary feeding were comparable in terms of swallowing rate, it is appropriate to consider why adult female herring gulls appear to be either selecting disturbed feeding or avoiding undisturbed feeding.

The extent of disturbed feeding by females is probably a result of their being competitively excluded from undisturbed feeding by males (see below).

However a factor which is important in determining the efficiency of disturbed feeding is manoeuvrability. Much of the material dumped at refuse tips is inedible. As the bulldozer moves backwards and forwards pushing the refuse into a pile, food items are temporarily exposed. The skill required is to move in quickly and snatch the item up without being run over. Females have a wing loading which is about 10% less than that of males and this indicates greater manoeuvrability, especially at low speeds. Females are therefore at an advantage over males when feeding behind the active bulldozer and this could relate to the preference which females showed for this type of feeding.

3.3.3 Feeding behaviour during undisturbed primary feeding

Peck rate

Females had a 25% greater peck rate than males, making on average 20 pecks/min compared with 16 pecks/min of males (Table 3.3).

Walking rate

Females had a 33% greater walking rate than males taking on average 32 paces/min compared with 24 paces/min of males (Table 3.4).

Swallowing rate

There was no overall difference in the rate at which males and females obtained food items (Table 3.3). However, in terms of the number of pecks and paces taken per food item swallowed, females had a more energetic foraging method, taking 32 pecks and 42 paces per food item swallowed compared with the 23 pecks and 33 paces of males.

Encounters

Males were more aggressive than females, making on average twice as many attacks per unit time (Table 3.3).However there was no difference in the rates at which they attacked

Table 3.3 Mean pecking, swallowing and attacking rates (± S.E.) of adult male and female herring gulls during undisturbed primary feeding at a refuse tip. The proportion of food obtained by attacking is also presented for each sex.

	Mean pecks/15s	Mean swallows/15s	Mean attacks/15s		Percentage of swallows obtained by attacking
			on adult	on immature	
Male	3.99 ± 0.27 (414)	0.18 ± 0.03 (414)	0.046 ± 0.008 (414)	0.019 ± 0.005 (414)	16.1 ± 3.8 (93)
Female	4.95 ± 0.23 (389)	0.16 ± 0.04 (389)	0.017 ± 0.006 (389)	0.012 ± 0.006 (389)	5.3 ± 2.6 (76)
Student's 't'	2.76	0.42[1])	2.13[1])	0.71[1])	2.35
P	<0.01	N.S.	<0.05	N.S.	<0.05

Sample sizes shown in parentheses. [1]) Student's 't' test performed on transformed data.

Table 3.4 Walking rates of male and female adult herring gulls.

Sex		Number of paces/15s				Total
		0	1–4	5–10	> 10	
Male	No.	4	171	162	77	414
	%	1	41	39	19	
Female	No.	0	122	157	110	389
	%	0	32	40	28	

Combining the zero and 1–4 paces/15s categories, the distributions for the two sexes are significantly different ($\chi^2_2 = 14.59$, $p < 0.001$).

immatures and the difference in attack rates was entirely accounted for by the difference in the rate at which the two sexes attacked other adults. Comparison of the relative proportions of attacks against different age classes with the average age structure of 73% adults observed during competitive feeding (Table 3.1) indicates a random distribution of male attacks with respect to the age of the attacked bird. However females attacked less adults and correspondingly more immatures than would be expected on the basis of a random attack distribution. When success in attack was defined either in terms of displacing the opponent or in terms of obtaining a food item as a result of an attack, no significant differences between the sexes in success rate were found. However, adult males obtained three times more of their food by attacking and displacing other herring gulls than did females (Table 3.3). In a minority of cases, this klepto-parasitism involved snatching a food item from the beak of another gull. More frequently, the attacking bird displaced another from its feeding patch and then began to feed there itself; thus it was more often the theft of a good feeding patch which was involved, rather than the theft of a food item. In the sample of data collected, adult females were not attacked significantly more frequently than adult males.

To summarise, females had an active independent foraging strategy with a high peck rate, high walking rate and low attack rate. Males, in contrast, obtained a greater proportion of their food by attacking and robbing other gulls and this was reflected in less independent foraging (i.e. lower pecking and walking rates) and a higher attacking rate.

Feeding position

In some cases, a clear edge and centre could be distinguished in the pile of refuse. In the edge area the refuse was more dispersed and often partially covered with earth. Edge feeding in this case was, therefore, similar to secondary foraging. Where these zones could be distinguished, the sexes of colour-marked adult herring gulls feeding in each zone were recorded. In the centre, 58% of herring gulls were males compared with 35% at the edge (Table 3.5).

3.3.4 Changes in feeding behaviour throughout the feeding bout

In a sample of 65 undisturbed primary feeding bouts, 60% lasted over 10 minutes and 32% continued for over 20 minutes. Feeding bouts were either terminated by some kind of disturbance, e.g. a person or a dog on the tip, a vehicle or a loud noise, or, on occasions, simply by the birds leaving for no obvious reason. As the feeding bout progressed, the proportion of males in the sample of colour-marked adults present increased significantly from 37% to 52% (χ^2_1 = 4.42, $p < 0.05$). That this change in sex ratio was the result of a net loss of females, and not a net gain of

Table 3.5 Number of sightings of individually colour-ringed male and female adult herring gulls feeding in the centre and edge areas of the refuse pile.

Feeding position		Sex		Total
		Male	Female	
Edge	No.	28	51	79
	%	35	65	
Centre	No.	22	16	38
	%	58	42	

$\chi^2_1 = 4.41$, $p < 0.05$

males, is suggested by the fact that the total number of herring gulls present tended to decrease as the feeding bout progressed. There was also a trend of increasing mean bill depth in males as the feeding bout progressed, (with no corresponding change in mean head and bill length), suggesting that older males were coming in later and/or younger males were leaving earlier (Fig.3.3). Although there was no overall difference between the sexes in the rate at which adults obtained food items, there were differences throughout the feeding bout. In the first ten minutes from the start of the feeding, the swallowing rates of adult males and females were similar. After this time, the swallowing rate of females declined significantly whilst that of males stayed constant, or even increased (Fig.3.4). Involvement of males in aggressive encounters was higher after the first ten minutes of feeding, both in terms of rate of attacking (Fig.3.5) and rate of being attacked (Fig. 3.6). There was no corresponding pattern or trend in the encounter rates of females (Figs. 3.5 & 3.6). To summarise, as the feeding bout progressed, the percentage of males increased; the data on bill depth suggests that the males present in the later stages were, on average, older and therefore more experienced foragers. At the same time, there was an increased rate of aggression. The change in sex ratio also indicates that some females were responding to the increased levels of aggression by leaving the feeding area.

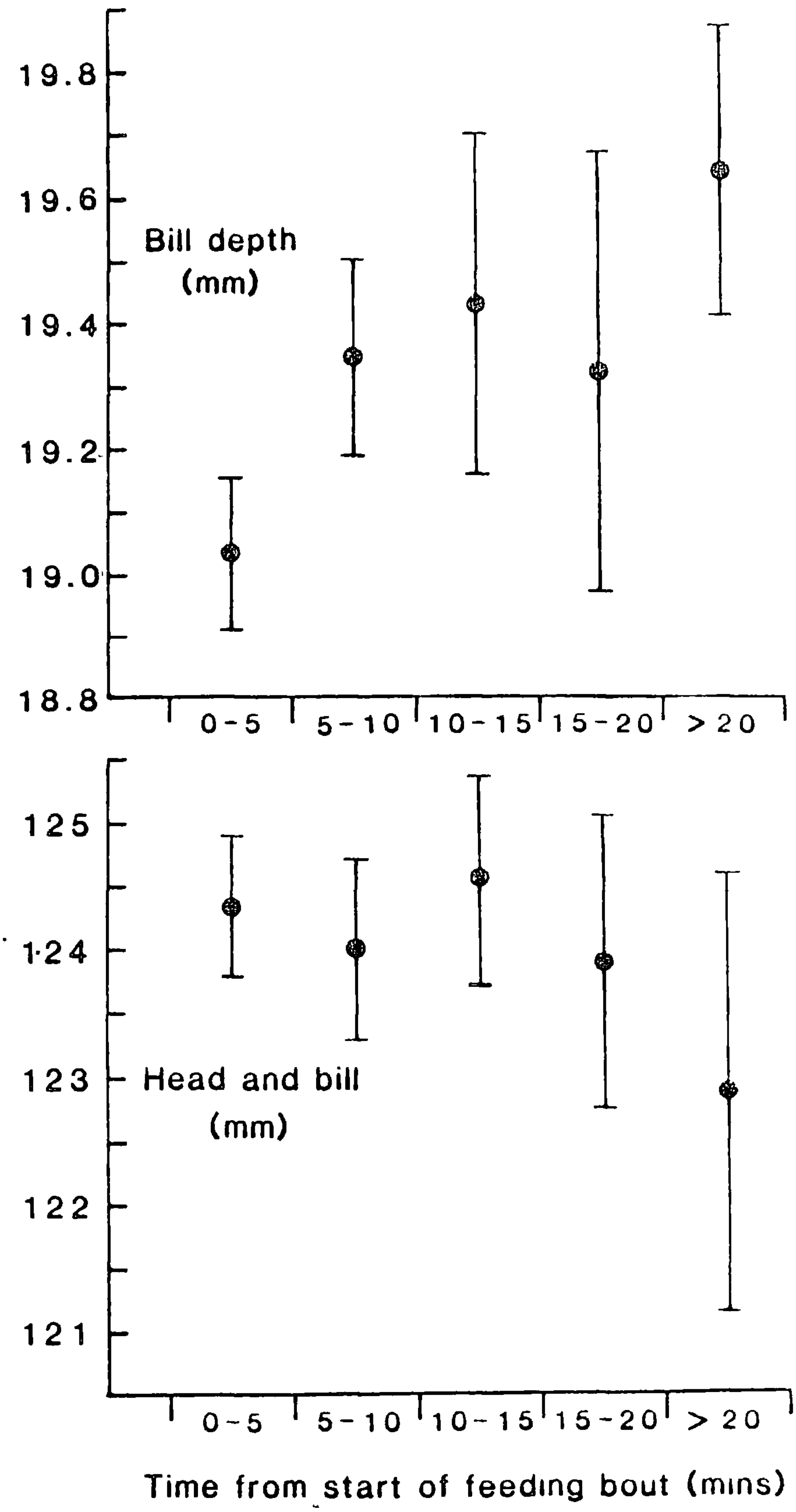

Fig. 3.3 Biometrics of adult male herring gulls present at 5 minute intervals throughout an undisturbed primary feeding bout.
(means ± 1 SE)
Difference between biometrics in first [illegible] minutes [illegible] ('t' tests). a) Bill depth, $t = 2.19$, $P < 0.05$, b) Head and bill length, $t = 0.85$, N.S.

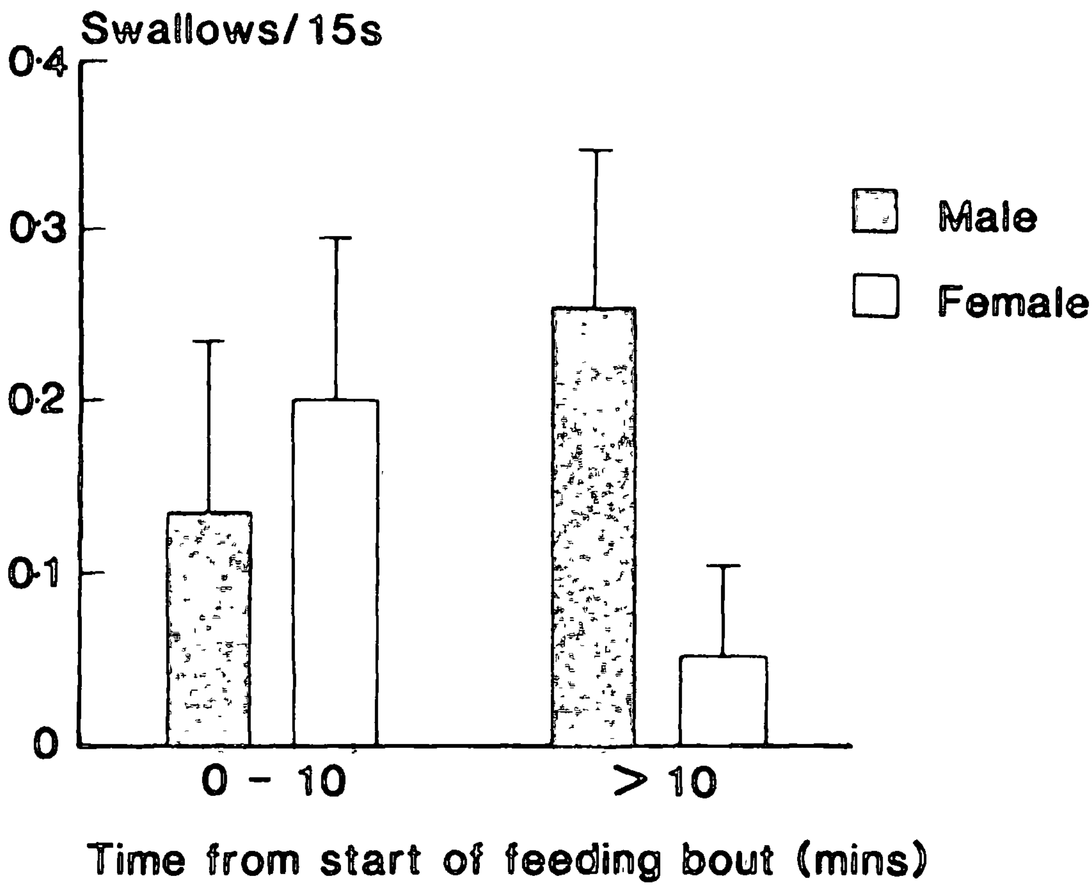

Fig. 3.4 Swallowing rates of male and female adult herring gulls throughout an undisturbed primary feeding bout (bars are 95% confidence limits). Difference between males and females (Student's 't' tests on transformed data):

0–10 mins	t = 0.93,	N.S.
>10 mins	t = 4.06,	$p < 0.001$

Difference between first ten minutes and later:

males	t = 1.80,	N.S.
females	t = 2.78,	$p < 0.01$

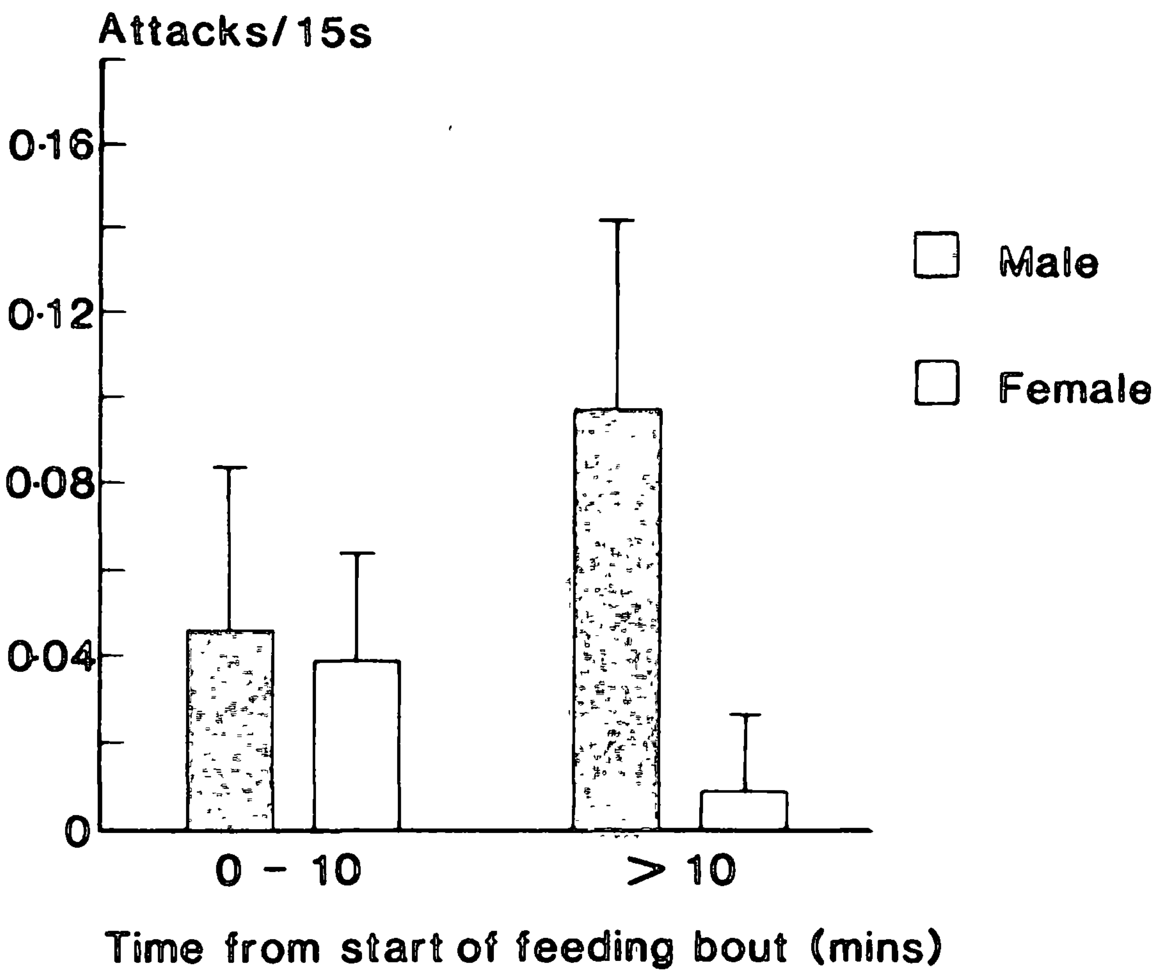

Fig. 3.5 Attacking rates of male and female adult herring gulls throughout an undisturbed primary feeding bout (bars are 95% confidence limits). Difference between males and females (Student's 't' tests on transformed data):

0–10 mins	t = 0.17,	N.S.
>10 mins	t = 3.67,	$p < 0.001$

Difference between first ten minutes and later·

males	t = 1.85,	N.S.
females	t = 2.14,	$p < 0.05$

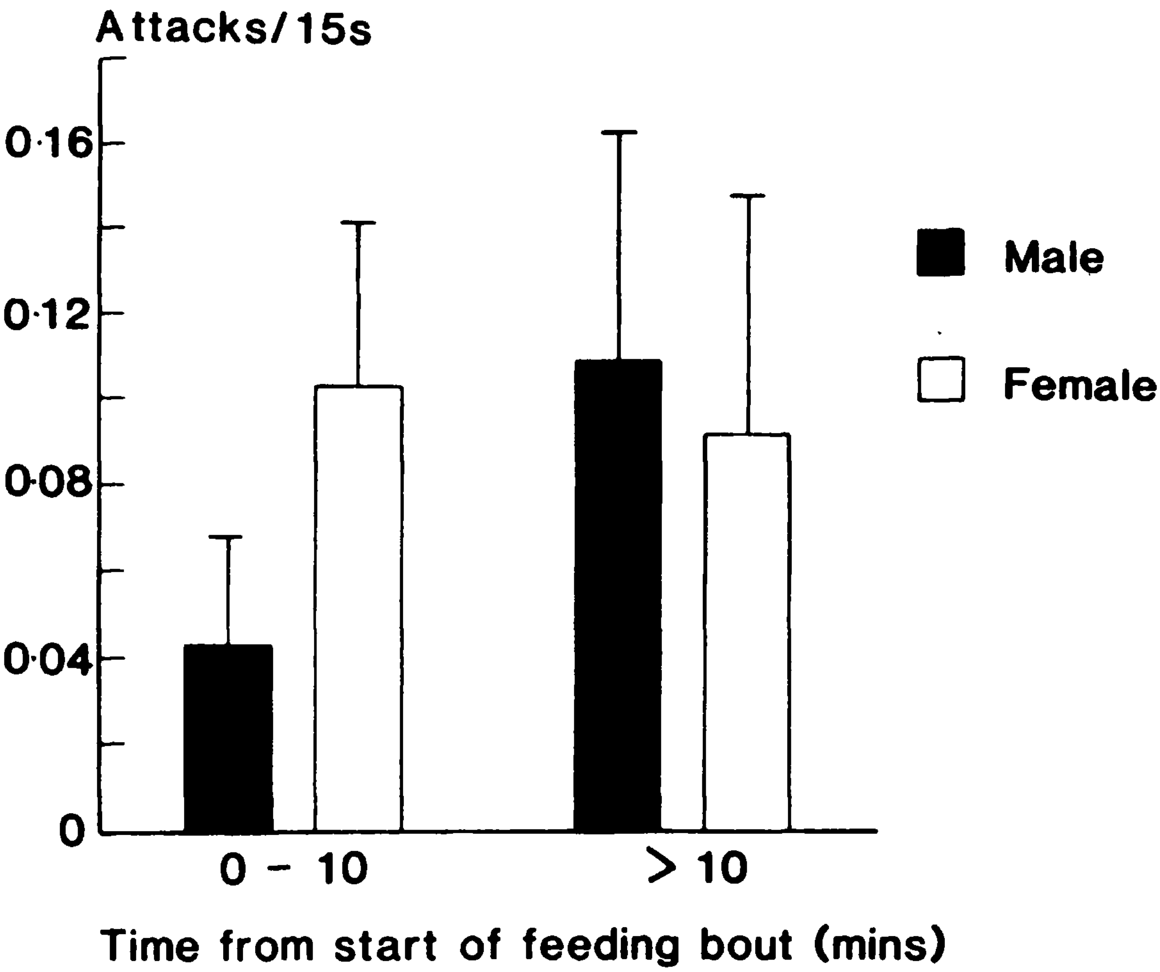

Fig. 3.6 Rate of being attacked for male and female adult herring gulls throughout an undisturbed primary feeding bout (bars are 95% confidence limits).

Difference between males and females (Student's 't' tests on transformed data):

0-10 mins	$t = 1.87$,	N.S.
>10 mins	$t = 1.46$,	N.S.

Difference between first ten minutes and later:

males	$t = 2.88$,	$p < 0.01$
females	$t = 0.23$,	N.S.

3.4 Discussion

A refuse tip provides a variety of feeding opportunities throughout the day. A herring gull can, within limits, choose when to feed and, in this way, may attempt to forage optimally, i.e. with minimum costs and maximum benefits. As the winter progressed, both sexes tended to increase the time spent feeding. This increase is probably due to decreased temperatures leading to increased energy requirements and possibly also the scarcity of other foods elsewhere. This trend was most marked in males, and may be a reflection of a change in the quality of the males which are present. The seasonal trend of decreasing mean bill depth suggests that the adult males present later in the winter are, on average, younger (the older males leave the wintering grounds first to go back to their breeding colonies). If the lower foraging success of younger herring gulls, shown for immature birds (VERBEEK 1977a; GREIG et al,. 1983), continues into adult life, then this may explain the greater seasonal increase in feeding time of males compared with females. Both sexes also showed a seasonal increase in the proportion of birds participating in undisturbed primary feeding. In this case it was the females in which the trend was most marked. Throughout the winter, the proportion of males at the tips decreased (COULSON et al., 1983c); in addition, the males present later in the winter may be, on average, younger. These two factors result in less competitive exclusion of females by males from primary undisturbed feeding as the winter progressed.

Evidence from several species of both birds and mammals indicates that body size is an important determinant of social dominance (FRETWELL 1969; APPLEBY, 1980). In higher vertebrates, males are usually larger than females and generally males are dominant over females (WILSON, 1975). In species where female dominance has been shown, e.g. hawks and owls (SNYDER & WILEY, 1976), hyenas (Crocuta crocuta; KRUK, 1972), the female is the larger sex. In this study, the larger male herring gull dominated the female in competitive feeding. In undisturbed feeding, adult male herring gulls showed an aggressive feeding strategy which involved obtaining at least a fifth of their food by attacking and displacing other feeding herring gulls from high quality feeding patches (Table 3.3). The benefits of stealing food items which other individuals have taken time to find has been shown in oystercatchers (Haematopus ostralegus; GOSS-CUSTARD et al., 1982), glaucous-winged gulls (Larus glaucescens; ROCKWELL, 1982), and in two egret species (CALDWELL, 1980). In the last study, CALDWELL also found that the benefit of winning was not simply in the short term gain of a single food item, but in the winning of a good foraging site which increased the rate of food intake subsequently.

In contrast, adult female herring gulls were subordinate in a competitive feeding situation. They attacked other herring gulls less, (particularly other adult herring gulls), and were attacked more. They fed more often in edge areas of the refuse pile, where food return was lower, but where aggressive interactions were also less frequent, (MONAGHAN, 1980). Although given the same feeding opportunities as males, they engaged more often in disturbed primary feeding which was less competitive. The competitive disadvantage of females became more apparent as the undisturbed primary feeding bout progressed. As good quality food patches became depleted, aggression increased and the rate at which females obtained food items fell. Some females responded by opting out of feeding there altogether. Adult males, in contrast, were able to sustain, or even to increase, their rate of food gain by increased reliance on obtaining food by attacking and displacing other birds i.e. increased use of klepto-parasitism.

In contrast, when herring gulls fed whilst the bulldozer was working, the bulldozer itself uncovered food items. The feeding method used in this situation is similar to surface dipping over water or feeding behind the plough. The herring gulls fly or run in, snatch up food items and fly off. If they land at all, it is only briefly. Competitive interactions between birds are therefore extremely rare (Table 3.1). Manoeuvrability is very important in this type of feeding, and here female herring gulls have an advantage over males because of their lower wing loading.

The inverse relationship between body size and manoeuvrability should hold for all geometrically similar animals since wing loading increases with body size and the power margin (the excess of power available over the power required) decreases (PENNYCUIK, 1972). In support of this, HORTON et al., (1983) found that, of five species of gulls feeding at tips, the smaller species i.e. black-headed and common gulls (Larus ridibundus, L. canus), were most adept at feeding close to the working bulldozer. BURGER (1981), in a study of laughing gulls (L. atricilla) and herring gulls feeding at a refuse tip, found that the smaller laughing gulls hovered around the working bulldozer and dipped for food items to a much greater extent than did the herring gulls.

SIBLY & McCLEERY (1983b) found that adult male herring gulls were more efficient foragers at refuse sites than females, measuring foraging efficiency in terms of rate of weight gain. In the present study, females, although subordinate to males in a competitive feeding situation, were able to compensate for their lowered efficiency by increased participation in disturbed feeding where competitive interactions were very infrequent. The relative performance of males and females will depend on the feeding opportunities which are presented during a visit to the tip. In the winter months, a herring gull may spend several hours of the day at a tip, and only feed for 30-40 minutes. To some extent, this is due to disturbance inhibiting the gulls from feeding. However, given the same feeding opportunities, males and females tend to make different choices. When additional constraints on feeding time such as incubation are in operation, this may severely limit the option of selecting particular types of feeding and may explain the lower feeding efficiency of females at tips during the breeding season (SIBLY & McCLEERY, 1983b). However, the exact relationships between body size, metabolic requirements and the energetic costs of different foraging methods requires further investigation.

4. COMPARATIVE FEEDING BEHAVIOUR OF THREE SPECIES OF WINTERING GULLS

4.1 Introduction

A foraging animal faces many decisions including where, when and how to feed. The choices made will depend, not only on the capabilities of the individual i.e. the physical constraints involved and the skills learnt, but also will be influenced by the choice made by other individuals.

A major physical constraint on foraging behaviour is body size. Body size can affect the size or weight of prey which can be killed or carried, or which it is profitable to take (e.g. Newton, 1979; Carlson & Moreno, 1983). Body size also has implications for flying ability, for example by affecting metabolic economy in flight (Bryant & Westerterp, 1982) or manoeuvrability at low speeds (Greenewalt, 1975). In many cases divergence in foraging behaviour between the sexes have been related to differences in body size (e.g. Erlinge, 1979; Newton & Marquiss, 1982), or occasionally more specifically to some aspect of body size such as bill length (Smith & Evans, 1973; Puttick, 1981). Where competitive interactions are important, dominant status may be related to body size. In a number of species social dominance of one sex by the other has been related to sexual size dimorphism (e.g. Harrison, 1983; Tilson & Hamilton, 1984; Greig et al., in press).

Mixed species feeding flocks add another parameter to the problem of how foraging decisions are made, that of how the species composition of the feeding flock may affect the behaviour of the component species: for example, in a study of feeding flocks of lapwings Vanellus vanellus, golden plovers, Pluvialis apricaria, and black-headed gulls, Larus ridibundus, on pasture, Barnard et al. (1982) found that the presence of black-headed gulls affected the relative feeding success of the other two species and their effects on each other.

The problems addressed in this paper concern the foraging decisions made by three species of gulls, in mixed species feeding flocks at refuse tips. The aim was to describe the behaviour of individuals of the three species throughout the winter and to interpret differences in behaviour and in foraging success in terms of the ways in which foraging decisions are made and foraging behaviour determined. Three species were investigated, the great black-backed gull, Larus marinus, herring gull, L. argentatus and black-headed gull, L ridibundus. During the winter in north-east England, British herring gulls, L. argentatus argenteus, are joined by herring gulls of Scandinavian origin, L. argentatus argentatus, the latter forming up to 30% of the feeding flock of gulls at tips in north east England in December and January (Coulson et al., 1984a). The Scandinavian herring gulls are larger and darker in mantle shade than their British counterparts (Barth, 1975). There is therefore a range in size in the feeding flock, namely, from largest to smallest, great black-backed gull, Scandinavian herring gull, British herring gull and black-headed gull. The numbers of each species which visit refuse tips each day are variable, as are the proportions in which they do so. Several workers have commented on differences between the behaviour of the three species at tips. Horton et al. (1983) recorded that black-headed gulls seemed to show a preference for feeding from the air and close to the working bulldozer, whereas the larger gulls preferred to feed when the tip was quiet. Verbeek (1979) in a study of herring, lesser black-backed, L. fuscus, and great black-backed gulls feeding at refuse tips commented that 'great black-backed gulls fed exclusively by parasitizing the other two gull species, especially herring gulls'. However, with the exception of the work of Barnard and his co-workers (Barnard & Stephens, 1981; Barnard et al., 1982; Thompson & Barnard, 1983), quantitative studies of multispecies feeding flocks in which flock dynamics (i.e. numbers and proportions of different species present) have been related to feeding methods and feeding success, have been lacking.

4.2 Methods

(a) Use of refuse tips

Counts were made of the number of great black-backed, herring and black-headed gulls at five refuse tips, namely Coxhoe, Tow Law, Consett, Greenside and Prudhoe, Co. Durham, on a total of 81 days between October 1982 and February

1983. All counts were made between 1130h and 1400h, when peak numbers of gulls were at the tips (Monaghan, 1980). Counts of herring gulls were divided into adults and immatures (1-4 years). Ages were not distinguished in the counts of great black-backed and black-headed gulls, but in both species the great majority were adults. In order to examine the effect of environmental conditions on the numbers of each species visiting tips, 14 environmental variables were used (listed in appendix A). Meteorological information for Tynemouth was obtained from the Newcastle Weather Centre and that for Durham City from the Durham University Observatory. Information on the size of the fish catch, landed daily at North Shields, was obtained from M.A.F.F. (North Shields).

(b) Feeding methods

Direct observations were made at Tow Law refuse tip, Co. Durham, between October 1982 and February 1983. A total of 13 complete daylight-hour observations (85 hours in all) were made at this refuse tip. Three types of feeding bout were distinguished as described in Greig _et al_. (in press), namely undisturbed primary, disturbed primary and secondary feeding. The main opportunity for undisturbed primary feeding was at lunchtime when the tip was quiet and birds fed on freshly dumped rubbish. Such feeding typically involved high density of birds. During disturbed primary feeding, the birds also fed at high density, but whilst the bulldozer was working. Such feeding was chaotic. Secondary feeding occurred mainly at the beginning and at the end of the day. The gulls fed at low density on dispersed rubbish which had been covered with earth. The number and types of feeding bouts, in which uniquely marked adult herring gulls participated, were recorded by direct observation. Morphological differences between males and females and between British and Scandinavian herring gulls have been used to identify both the sex and race of the individually marked birds (Coulson et al., 1984a). Data were collected on 159 adult British herring gulls and 39 adult Scandinavian herring gulls. Counts were made of the number of each species participating, 2-5 minutes from the start of feeding, in a total of 99 feeding bouts.

(c) Foraging behaviour

Data on the foraging behaviour of individuals of each species were obtained using colour-video recordings, made at five refuse tips (Coxhoe, Wingate, Hett Hills, Consett and Tow Law, Co. Durham). These recordings were made between October 1981 and February 1982 and October 1982 and February 1983. Data were collected on unmarked individuals of each species, for all three types of feeding. Data on individually colour-ringed adult herring gulls were collected during undisturbed primary feeding only. An observation unit of 15 seconds was used in the analysis of video recordings, and the following data were collected on each individual, in each unit: (a) number of pecks, (b) number of food items swallowed, (c) number of paces ranked in one of four categories; 0 - none, 1 - one to four, 2 - five to ten, 3 - over ten: mean walking rates were estimated by assigning the following number of paces to each rank; 1 - 2.5, 2 - 7.5, 3 - 15, (d) proportion of time spent standing still scanning the feeding birds and (e) proportion of time spent in the air, both ranked in one of four categories; 0 - none, 1 - 1-5s, 2 - 6-10s, 3 - 11-15s: means for both (d) and (f) were estimated by assigning the following number of seconds to each rank; 1 - 2.5, 2 - 7.5, 3 - 12.5, (f) number and nature of encounters with other birds. The statistical methods used in the analysis of the behavioural data followed those described by Greig et al. (in press).

4.3 Results

4.3.1 Use of tips by great black-backed, herring and black-headed gulls

Both the absolute numbers of the three species present and their relative proportions were variable. The majority of gulls found feeding at refuse sites in this study were herring gulls (Table 4.1). Adult and immature herring gulls visited tips in varying proportions but the great majority of great black-backed and black-headed gulls present were adults. Since the standard deviation of the numbers present varied with the mean for all three species, a logarithmic transformation was used in order to test the equality of the coefficients of variation. The numbers of both great black-backed and black-headed gulls were significantly more variable than those of either adult or immature herring

Table 4.1 Average numbers of three gull species at five refuse tips daily throughout the winter (means ± SD).

Tip	No. days observation	Great black-backed gull	Adult herring gull	Immature herring gull	Black-headed gull
Coxhoe	24	18 ± 22	281 ± 278	88 ± 82	92 ± 127
Greenside	8	23 ± 30	177 ± 145	107 ± 111	143 ± 99
Consett	25	26 ± 27	182 ± 146	110 ± 80	233 ± 143
Prudhoe	7	48 ± 40	264 ± 157	156 ± 78	223 ± 106
Tow Law	17	41 ± 33	232 ± 126	100 ± 71	76 ± 52
All Tips	81	28 ± 30	228 ± 193	105 ± 82	148 ± 134
Variance In nos.	81	2.264	1.1553	0.9304	1.955

Comparisons of variability between species (d.f. = 79,79)

	Adult herring gull	Immature herring gull
Great black-backed gull	$F=1.96$, $p < 0.01$	$F=2.43$, $p < 0.01$
Black-headed gull	$F=1.69$, $p < 0.05$	$F=2.10$, $p < 0.01$

gulls (Table 4.1). In order to investigate the relationships, if any, between day to day variation in the numbers of the different species visiting tips and environmental conditions, the technique of multiple regression was used.

There were significant differences both between tips ($F=2.77$, d.f.=4.76, $p < 0.05$) and months ($F=5.78$, d.f.=4.76, $p < 0.001$) in the number of great black-backed gulls present, with significantly greater numbers being present in January than in all other months. The data, considered for both adult and immature herring gulls, showed no significant differences between tips ($F=1.02$ and $F=0.99$ respectively) but the seasonal effect was present, again significantly higher numbers being present in January (adults; $F=11.21$, d.f.=4.76, $p < 0.001$: immatures; $F=6.40$, d.f.=4.76, $p < 0.001$). There were no seasonal differences in the total number of black-headed gulls present ($F=1.90$, d.f.=4.76, n.s.), but there were large differences between numbers at different tips ($F=7.05$, d.f.=4.76, $p < 0.001$).

A stepwise multiple regression was performed using the number of each species as the dependent variable and six independent variables which had significant ($p < 0.05$) simple correlations with the number of one or more species. (See Appendix A for complete list of environmental variables examined.) First, in order to remove the variation due to differences between tips and between January and the other months, these variables were forced in at the beginning of the regression. The results of the regression analysis for each of the three species (adult and immature herring gulls were considered separately) are shown in Table 4.2 together with the range of values observed for each environmental variable.

Three variables had significant correlations with great black-backed numbers, namely the size of the fish catch, wind speed (measured at 0600h) and whether or not there was an overnight frost. The negative relationship with fish catch was such that a 20 fold increase in the size of the fish catch would predict a reduction in the number of great black-backs at the tips by twelve birds, a decrease of 43% on the mean number present. The effect of wind speed was positive and indicated that a change from calm conditions to gale force winds (34 knots) would result in an increase of 25 in the number of great black-backs present. Overnight frost also had a positive effect on numbers inland, leading to an increase of 12 birds.

The two variables which had a significant influence on adult herring gull numbers at tips were wind speed (measured at 1800h on the previous day) and temperature at 0600h. The two wind speed variables (0600h and 1800h) were significantly correlated ($r=0.46$, d.f.=79, $p < 0.01$) as were the frost and temperature variables ($r=0.74$, d.f.=79, $p < 0.01$). Herring gulls were therefore similar to great black-backed gulls in that cold and windy conditions resulted in larger numbers feeding at tips. A change from calm to gale force winds predicted an increase of 124 adult herring gulls

Table 4.2 Results of stepwise multiple regression of numbers of three gull species against a group of environmental variables, after inclusion of dummy variables coding for tip and month. The range of values recorded for each environmental variable is also given.

Species	Step	Independent variable	Range	Multiple r-square	Regression coefficient	Standard error
Great black-backed gull	0	Dummies	-	0.362	-	-
	1	Log fish catch	0 - 8.24	0.439	-3.99	1.35
	2	Wind speed (0600h)	0 - 50	0.479	0.72	0.34
	3	Frost	0 - no frost 1 - frost	0.509	12.00	5.12
Adult herring gull	0	Dummies	-	0.320	-	-
	1	Temperature (0600h)	-2 - 12	0.453	-17.12	4.68
	2	Wind speed (1800h)	0 - 50	0.485	3.65	1.70
Immature herring gull	0	Dummies	-	0.211	-	-
	1	Wind speed (1800h)	0 - 50	0.276	2.11	0.82
Black-headed gull	0	Dummies	-	0.354	-	-
	1	Wind direction	0 - offshore 1 - onshore	0.394	73.5	33.3

(an increase of 54% on the mean number present), and a one degree centigrade decrease in temperature an increase of 17 (8% of the mean) in the number of adult herring gulls feeding at tips. Wind speed also had a significant effect on numbers of immature herring gulls, but for this group there was no significant effect of temperature. Although the numerical effect of a change in wind speed was less for immatures than for adults (calm to gale force predicts an increase of 72), the proportional effect was similar.

None of the environmental variables proved useful in predicting the number of black-headed gulls at tips from day to day. The only significant variable was wind direction, with onshore winds resulting in an increase of 74 (±33) black-headed gulls. However, differences between tips and months explained 35% of the variation in numbers, and wind direction was responsible for only a further 4% of the variation in number.

The seasonal effect resulting in larger numbers of both herring and great black-backed gulls being present in January was examined to determine whether it could be explained by changes in any of the environmental variables shown to be predictors of the numbers of these two species. The only variable which showed a significant difference between January and the other months was the size of the fish catch, the average catch in January being 16% of that over the rest of the winter season (Student's 't' test of log fish catch; $t=2.42$, d.f.$=79$, $p < 0.025$). When the size of fish catch variable was forced in at the start of the regression, a significant seasonal effect remained for both species. Therefore higher numbers of great black-backed and herring gulls feeding at tips in January was not explicable in terms of changes in temperature, wind speed or the size of the fish catch, and it is likely that other factors relating to larger scale winter movements were responsible.

In summary, cold and windy (i.e. chilly) conditions resulted in higher numbers of both great black-backed and herring gulls feeding at refuse tips. Changes in wind speed had a proportionally greater effect on great black-backed gull numbers, whereas those of adult herring gulls were more influenced by changes in temperature. In great black-backed gulls alone, the size of the fish catch was important in determining numbers at tips. Great black-backed gulls also differed from herring gulls in that there were significant differences in numbers at different tips, and since the two species responded differently, it seems unlikely that this can be explained in terms of the size or capacity of the tips. In black-headed gulls this 'tip effect' was responsible for nearly all the variation in numbers which was explained in the analysis. Again there was no common pattern to indicate a simple effect of tip size. Factors such as proximity to the coast or to night time roosts, the size of the loafing area and availability of water (for drinking) are all likely to be important. In addition, the working regime of the refuse tip may influence feeding methods, and in this way favour one species more than another. The feeding methods used by the three species are discussed in the following sections.

4.3.2 Feeding methods

The relative proportions of the three gull species which participated in undisturbed primary, disturbed primary and secondary feeding are shown in Table 4.3 It is evident that, for all three types of feeding, the proportions of each of the three species present departed from that expected if feeding methods were chosen at random. Thus, herring gulls were found in higher than expected proportions in undisturbed primary feeding and in lower than expected proportions in disturbed primary feeding and lower still in secondary feeding. Great black-backed gulls selected secondary feeding and usually avoided disturbed primary feeding. The pattern in black-headed gulls was different again; a (much) greater than expected proportion participating in disturbed primary and secondary feeding and a lower than expected proportion being found in undisturbed primary feeding.

Records of sightings of colour-ringed birds were used to investigate the use of different feeding methods by British and Scandinavian herring gulls. There were no differences in the proportions of feeding birds of each race which participated in undisturbed primary or in secondary feeding. However 46% (n=317) of feeding British herring

Table 4.3 Proportions of the three gull species in each of three types of feeding (sample sizes refer to number of feeding bouts on which observations were made). The average numbers of each species present each day is also given.

Feeding type	Herring gull			Great black-backed gull			Black-headed gull		
	Mean	SE	%	Mean	SE	%	Mean	SE	%
Undisturbed primary n = 43	100	8	83	11	1	9	9	2	8
Disturbed primary n = 20	45	8	55	<1		<1	38	8	45
Secondary n = 36	14	2	34	5	2	13	21	3	53
Total numbers present (n = 14)	378	43	75	46	8	9	80	14	16

gulls participated in disturbed primary feeding compared to 36% (n=104) of feeding Scandinavian herring gulls; further, on eleven out of thirteen days the proportion of feeding British birds using this feeding method was higher than that for Scandinavian birds (binomial probability, p=0.022).

4.3.3 Feeding behaviour during secondary feeding

Aspects of the feeding behaviour of individuals of the three species during secondary feeding are shown in Table 4.4 Great black-backed gulls had significantly higher peck, swallow and encounter rates than either of the other two species. In contrast herring and black-headed gulls had significantly higher walking rates than did great black-backs, and there was no difference in the proportion of time each species spent standing still, scanning the other feeding birds. Thus, during secondary feeding great black-backed gulls foraged more effectively than the other two species and obtained a high proportion (58%, n=38) of their food by robbing other feeding gulls (mostly herring gulls). Secondary feeding was relatively unprofitable for both herring and black-headed gulls (see later for comparisons with other feeding methods), who patrolled the feeding area extensively but obtained very little food for their efforts. None of the three species spent time in the air during secondary foraging.

4.3.4 Feeding behaviour during disturbed primary feeding

Since great black-backed gulls so rarely participated

Table 4.4 Feeding behaviour of three gull species during secondary feeding (means ± SE).

	Black-headed gull	Herring gull	Great black-backed gull
	n=42	n=25	n=61
Pecks/15s	2.74 ± 0.54	3.12 ± 0.45	4.21 ± 0.57
Swallows/15s	0.02 ± 0.02	0.06 ± 0.04	0.46 ± 0.10
Encounters/15s	0.12 ± 0.05	0.04 ± 0.04	0.21 ± 0.04
*Paces/15s	12.5	10.8	4.5
*% time standing	3.0	5.3	3.8

Significance:	Pecks	Swallows	Encounters	Paces
GBB vs HG	t=1.52, n.s.	t=3.32, $p < 0.01$	t=2.38, $p < 0.01$	$\chi^2_2 = 27.9$, $p < 0.001$
GBB vs BHG	t=1.88, n.s.	t=4.02, $p < 0.001$	t=1.28, n.s.	$\chi^2_2 = 52.3$, $p < 0.001$
BHG vs HG	n.s.	n.s.	n.s.	n.s.

* means estimated from categorical data (see methods)

in disturbed primary feeding (Table 4.3), no data are presented for this species in this section. The feeding behaviour of herring and black-headed gulls during disturbed primary feeding is compared in Table 4.5. The most striking differences were in peck rate and in the proportion of time spent in the air, hovering over the feeding area. The significantly lower peck rate and higher proportion of hovering time in black-headed gulls reflects the 'surface dipping' method of feeding. Black-headed gulls hovered over the feeding area and periodically dipped down and snatched up food items as they were exposed by the working bulldozer. Herring gulls used this method to a lesser extent, and tended to spend more time on the ground searching; hence their higher peck rate. Although herring gulls hovered less than black-headed gulls, they still spent over a quarter of the time in the air, a considerably greater proportion than during any other feeding method. There was no difference in average swallow rate between the two species.

4.3.5 Feeding behaviour during undisturbed primary feeding

Aspects of the feeding behaviour of great black-backed, Scandinavian herring, British herring and black-headed gulls during undisturbed primary feeding are shown in Table 4.6 Although data are presented for black-headed gulls, their participation in undisturbed primary feeding was limited to 1-2 minutes at the start of the feeding bout; hence the very low average numbers of this species in this type of feeding (Table 4.3). Typically, black-headed gulls were the first to

Table 4.5 Feeding behaviour of herring and black-headed gulls during disturbed primary feeding (means ± SE).

	Herring gull (n=43)	Black-headed gull (n=106)	significance
Pecks/15s	3.49 ± 0.37	1.67 ± 0.30	$t=3.86$, $p < 0.01$
Swallows/15s	0.28 ± 0.11	0.15 ± 0.06	n.s.
*Paces/15s	6.6	7.2	n.s.
Encounters/15s	0.02 ± 0.02	0	n.s.
*% time in air	26	73	$\chi^2_2=46.4$, $p < 0.001$

* means estimated from categorical data (see methods)

Table 4.6 Feeding behaviour of three species of gull during undisturbed primary feeding (means ± SE).

	Black-headed gull	British herring gull	Scandinavian herring gull	Great black-backed gull
	n=140	n=763	n=166	n=900
Pecks/15s	4.40 ± 0.26	4.39 ± 0.18	3.38 ± 0.44	3.05 ± 0.15
Swallows/15s	0.28 ± 0.04	0.17 ± 0.02	0.17 ± 0.04	0.28 ± 0.04
*Paces/15s	5.1	7.2	5.9	6.2
Rate of attacking	0.034 ± 0.016	0.051 ± 0.008	0.119 ± 0.026	0.243 ± 0.016
Rate of being attacked	0.097 ± 0.036	0.113 ± 0.004	0.119 ± 0.047	0.049 ± 0.010
*% time standing	2.0	3.6	18.0	13.5
*% time in air	24.0	0.8	0.8	0.0
% food obtained by attack	2 (n=45)	11 (n=167)	22 (n=36)	60 (n=328)

significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

	Swallow rate	Attack rate	Rate of being attacked	% food from interaction
GBB vs BrHG	*	***	***	***
GBB vs ScHG	n.s.	***	n.s.	***

	Walking rate	Peck rate	Attack rate	% time standing still
BrHG vs ScHG	**	*	**	**

* means estimated from categorical data (see methods)

move in to feed, but within 1-2 mins nearly all had been displaced, apparently excluded by the larger gulls. However, direct aggressive encounters between black-headed and herring gulls were rare and no encounters between them and great black-backed gulls were observed. Black-headed gulls spent a high proportion of time in the air, landing for very short periods only. This reduced direct contact between them and the larger gull species and as the numbers of herring and great black-backed gulls built up, black-headed gulls were inhibited from landing at all. Thus, the lack of black-headed gulls in undisturbed primary feeding may be a result of their avoidance of the larger gulls, rather than direct competitive exclusion. Although the swallowing rate achieved by black-headed gulls in this type of feeding was relatively high, it was only sustained for a very short time, and therefore the total food gain was small.

With the exception of the first one or two minutes, herring and great black-backed gulls comprised 92% of the feeding flock in undisturbed primary feeding (Table 4.3). Great black-backed gulls had, on average, a significantly higher swallowing rate of one and a half times that of either race of herring gull (Table 4.6). They made four times as many attacks per unit time as British herring gulls and twice as many as Scandinavian herring gulls (Table 4.6). In addition, the rate at which individual great black-backed gulls were attacked was half that for either race of herring gull (Table 4.6). The most marked difference between the two species was in the proportion of food obtained by attack, i.e. in the use of kleptoparasitism. Three fifths of food items obtained by great black-backed gulls were either stolen directly from other gulls or, more often, obtained from a feeding patch which was acquired by displacing another successfully feeding bird. The corresponding proportions for Scandinavian and British herring gulls were a fifth and a tenth, respectively (Table 4.6). Low pecking and walking rates, high attack rates and a high proportion of time spent standing still were all behaviours which correlated with a high level of kleptoparasitism. Although the difference in the proportion of food gained by attack between British and Scandinavian herring gulls was not significant, Scandinavian herring gulls had walking and pecking rates which were similar to those of great black-backs, and which were significantly lower than those of British herring gulls (Table 4.6). They also had a significantly higher attack rate and spent a greater proportion of time standing still than British birds (Table 4.6). This evidence suggests increased use of klepto-parasitism by Scandinavian herring gulls. However, there were no differences between the two races in mean swallowing rate (Table 4.6). Increased use of kleptoparasitism by great black-backed gulls did lead to increased foraging success. A comparison of the ratio of attacks made to attacks suffered (if, as was true in this case, there are no differences in success) gives an indication of competitive ability. Individual great black-backed gulls made significantly more attacks than they suffered, due to the apparent reluctance of herring gulls to attack them (Table 4.6). This suggests they were able to commandeer the most profitable feeding patches on the refuse and, in this way, to achieve a higher swallowing rate than either race of herring gull.

4.3.6 Comparison of participation and performance with respect to feeding method

1. Great black-backed gulls: There was no difference in the swallowing rates achieved during secondary and undisturbed primary feeding (Tables 4.4 & 4.6). This is surprising given the more dispersed and covered nature of the refuse during secondary feeding. The significantly higher peck rate in secondary feeding ($t=1.99$, $d.f.=959$, $p < 0.05$) reflects the greater effort required to uncover and extract edible items. However, the rates of aggression and the extent of klepto-parasitism were comparable in the two feeding types (Tables 4.4 & 4.6).The data on the proportions of each species using the different feeding methods (Table 4.3) indicate that the proportion of great black-backed gulls which participated in secondary feeding was higher than that of herring or black-headed gulls. Thus increased participation was associated with increased success, which would be predicted by optimal foraging theory, if maximising food intake i.e. swallowing

rate, was the goal.

2. Herring gulls: Both types of primary feeding were comparable in terms of average swallowing rate (Tables 4.5 & 4.6) but a comparison of the variance indicates that the reward in disturbed feeding was significantly more variable ($F=2.21$, d.f.=42.762, $p < 0.01$). The main differences between these two feeding methods were that undisturbed feeding was considerably more competitive, with an eight times higher encounter rate, and that the time available for undisturbed feeding was greater (Greig et al., in press). Secondary feeding involved a lower food return but had the advantage of being less competitive and also being available for a greater period of time (Greig et al., in press). Table 4.3 shows that herring gulls demonstrated an order of preference in feeding type (namely: undisturbed primary > disturbed primary > secondary) which agrees with their performance, if maximising food intake and minimising the uncertainty of feeding success are the most important considerations. Manoeuvrability is also an important factor in disturbed feeding and the lower proportion of Scandinavian herring gulls which used this feeding method may be a consequence of energetic constraints due to greater body size.

3. Black-headed gulls: As with the herring gull, both types of primary feeding were comparable in terms of average swallowing rate (Tables 4.5 & 4.6) but the reward in disturbed feeding was significantly more variable ($F=1.80$,

d.f.=105,139, $p < 0.05$). The average swallowing rate during secondary feeding was significantly lower than that during undisturbed primary feeding (Tables 4.4&4.6 ; t=5.49, d.f.=180, $p < 0.001$). The order of preference in feeding type demonstrated by black-headed gulls was; disturbed primary > secondary > undisturbed primary. Thus if maximising food intake was the only consideration, they were clearly not behaving optimally. However smaller size and therefore lower wing loading affords black-headed gulls an energetic advantage over the larger gulls during disturbed feeding. Despite their high swallowing rate, black-headed gulls took little part in undisturbed primary feeding. This was either due to direct competitive exclusion by the larger gulls, or, more probably, a result of the black-headed gulls avoiding the concentrations of the larger gulls. When the larger species were absent or greatly outnumbered by black-headed gulls, the latter participated fully in undisturbed feeding (personal observation; Horton et al., 1983).

4.3.7 Relative importance of different feeding methods to each species

The average proportion of food obtained daily by different feeding methods can be partitioned for each species, using (a) the average reward per individual in each feeding method (Tables 4.4-6), (b) the mean daily duration of each type of feeding (Greig et al., in press), and (c) the proportion of each species present which used each feeding method (Table 4.3). The average daily food gain per individual for each feeding method is then given by the product of (a), (b) and (c). The relative importance of each feeding method to each species is thus based on a combination of the average feeding success using that feeding method, the availability of that type of feeding and the proportion of the species which participated. Although there are large errors attached to these estimates, this analysis does allow the relative importance of each feeding method to be compared both within and between species (Table 4.7). Disturbed feeding was of greatest importance to black-headed gulls; despite its limited availability of only 22 minutes per day, 75% of food was obtained using this feeding method. Herring gulls, in contrast, obtained nearly all (81%) of their food during undisturbed primary feeding, most of the balance from disturbed feeding, and very little at all from secondary feeding (Table 4.7). Great black-backed gulls also obtained a high proportion of food from undisturbed primary feeding, although less than the corresponding proportion for herring gulls. Secondary feeding was of considerably more importance to great black-backed gulls than to either of the other two species (Table 4.7). The relative metabolic size of herring and great black-backed gulls is such that great black-backed gulls require approximately 60% more food than herring gulls. Whereas herring gulls may be able to meet their food needs during primary feeding, it may be that, due to the limited availability of undisturbed feeding and the disadvantage incurred by large body size in disturbed

Table 4.7 The proportion of food obtained by different feeding methods each day partitioned for each species.

Species	Feeding method		
	Undisturbed primary	Disturbed primary	Secondary
Black-headed gull	0.13	0.74	0.13
Herring gull	0.81	0.16	0.03
Great black-backed gull	0.67	-	0.33

feeding, great black-backed gulls cannot. They may compensate by increased use of secondary foraging.

4.3.8 Effect of body size on feeding behaviour

The extent of participation in disturbed feeding was clearly influenced by body size. There was a trend of decreasing participation with size, from black-headed gull, British herring gull, Scandinavian herring gull to great black-backed gull. In addition, within each race of herring gull there was a difference between the sexes, with proportionately more females participating in disturbed feeding. There was a significant negative correlation between wing loading (estimated by body weight/wing length^2) and participation in disturbed feeding (Fig. 4.1). Wing loading acts as a constraint on the ability to manoeuvre especially at low speeds (Greenewalt, 1975). In disturbed feeding both black-headed and herring gulls spent a high proportion of time hovering (Table 4.5) and made repeated landings and take-offs. The relatively high wing loading of great black-backs apparently made it unprofitable to attempt participation in disturbed feeding, under the conditions investigated in this study. In the same way, the significantly lower participation of Scandinavian herring gulls in disturbed feeding compared to British herring gulls can be explained by differences in wing loading.

Competitive ability is directly related to body size. It is evident that several aspects of feeding behaviour

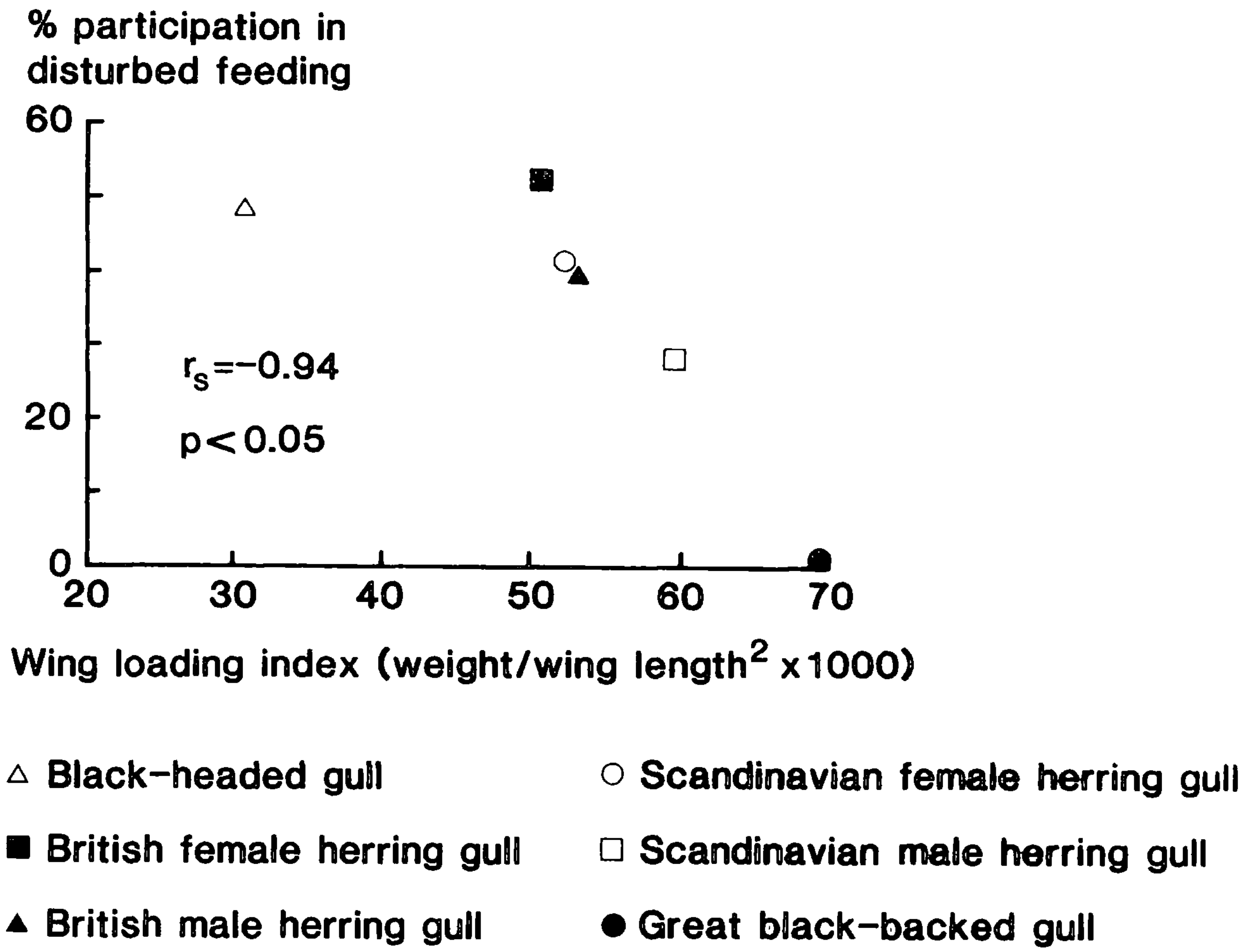

Fig. 4.1 Participation in disturbed feeding and wing loading. (Data for herring gulls are based on the proportion of feeding colour-ringed birds which participated in disturbed feeding. Those for black-headed gulls and great black-backed gulls are based on the ratio of the average number participating in disturbed feeding each day to the average total number of that species present at the tip.)

during undisturbed primary feeding show trends which are size-related (Table 4.6). The foraging behaviour of males and females of both races of herring gull during undisturbed primary feeding showed similar size related trends (Table 4.8). The British male and the Scandinavian female are of similar size and the similarity of their foraging behaviour indicates that sex-related differences in both races are determined primarily by size rather than by sex. Peck rates, of all three species, and walking rates, of herring and great black-backed gulls decreased with increasing size (Tables 4.6 & 4.8). Aggression was significantly and positively correlated with size ($p < 0.01$), as was the proportion of food obtained by attacking and displacing other feeding birds (Fig. 4.2). However, feeding success, as measured by swallowing rate, was not size-related (Fig. 4.3). The high feeding success of black-headed gulls was only achieved at the start of the feeding bout, after which time very few black-headed gulls participated. There were no significant differences in swallowing rate between the sexes or races of herring gulls although one might have expected that, in competitive feeding, larger birds would be dominant and therefore more successful. One explanation is that subordinate individuals may opt out of competitive feeding as soon as their feeding rate declines, and compensate by feeding in other ways. Indeed, this describes the behaviour of black-headed gulls, which compensate by increased secondary and disturbed primary feeding. There is evidence

Table 4.8 Comparison of feeding behaviour of British and Scandinavian herring gulls of both sexes (means ± SE)

	British female	British male	Scandinavian female	Scandinavian male
	n=366	n=391	n=95	n=71
Pecks/15s	4.98 ± 0.21	3.88 ± 0.27	3.92 ± 0.61	2.66 ± 0.52
*Paces/15s	7.7	6.7	6.5	5.0
Swallows/15s	0.166 ± 0.051	0.184 ± 0.034	0.197 ± 0.048	0.128 ± 0.043
Attacking rate	0.032 ± 0.010	0.067 ± 0.013	0.094 ± 0.032	0.156 ± 0.043
Rate of being attacked by HG	0.097 ± 0.021	0.069 ± 0.013	0.057 ± 0.028	0.071 ± 0.029
Rate of being attacked by GBB	0.016 ± 0.008	0.042 ± 0.011	0.026 ± 0.064	0.096 ± 0.040
% food obtained by attack	5 (n=76)	16 (n=91)	17 (n=23)	31 (n=13)

* means estimated from categorical data (see methods)

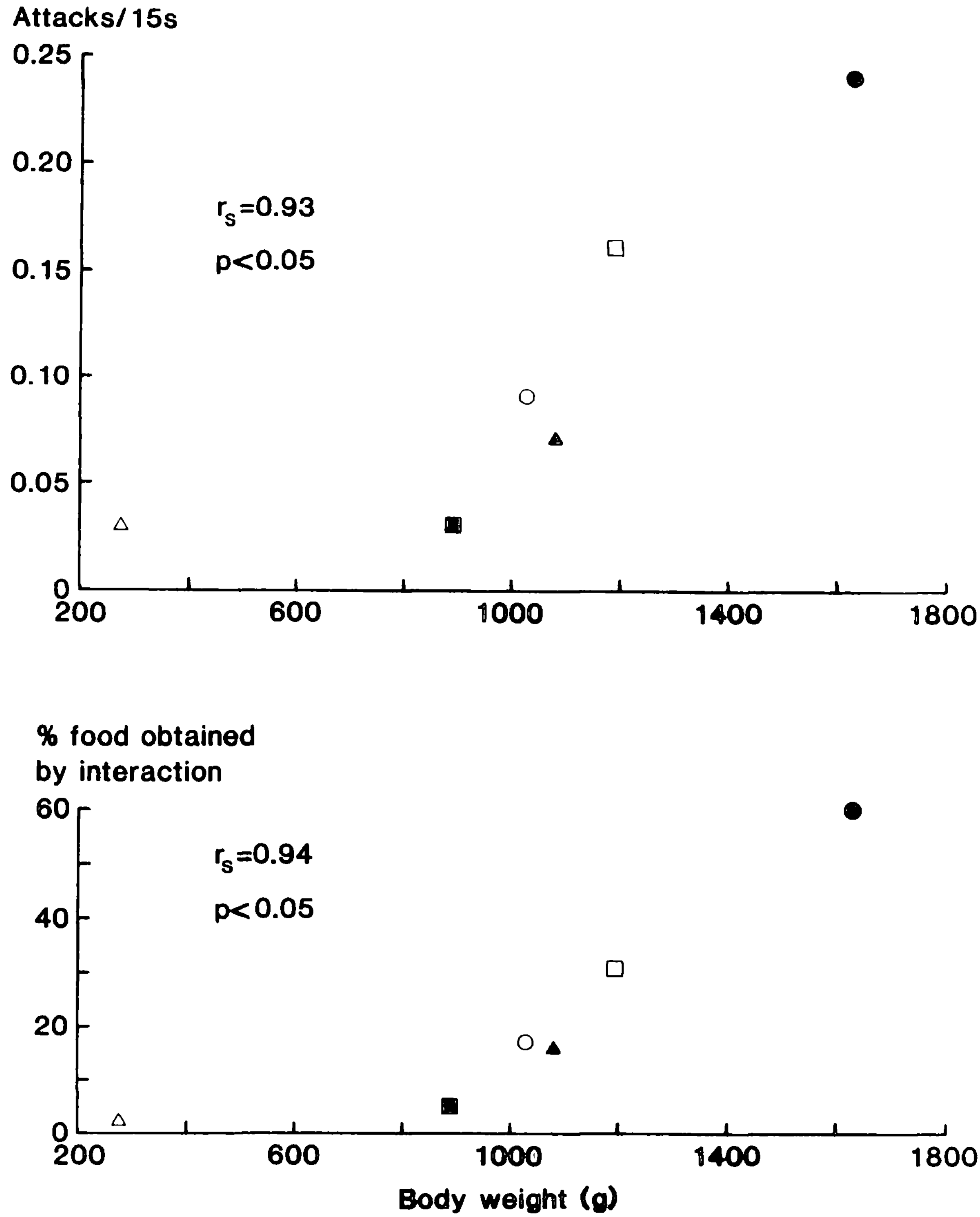

Fig. 4.2 Variation in a) attacking rate and b) proportion of food gained by interaction, with body weight. (For key to symbols see Fig. 4.1)

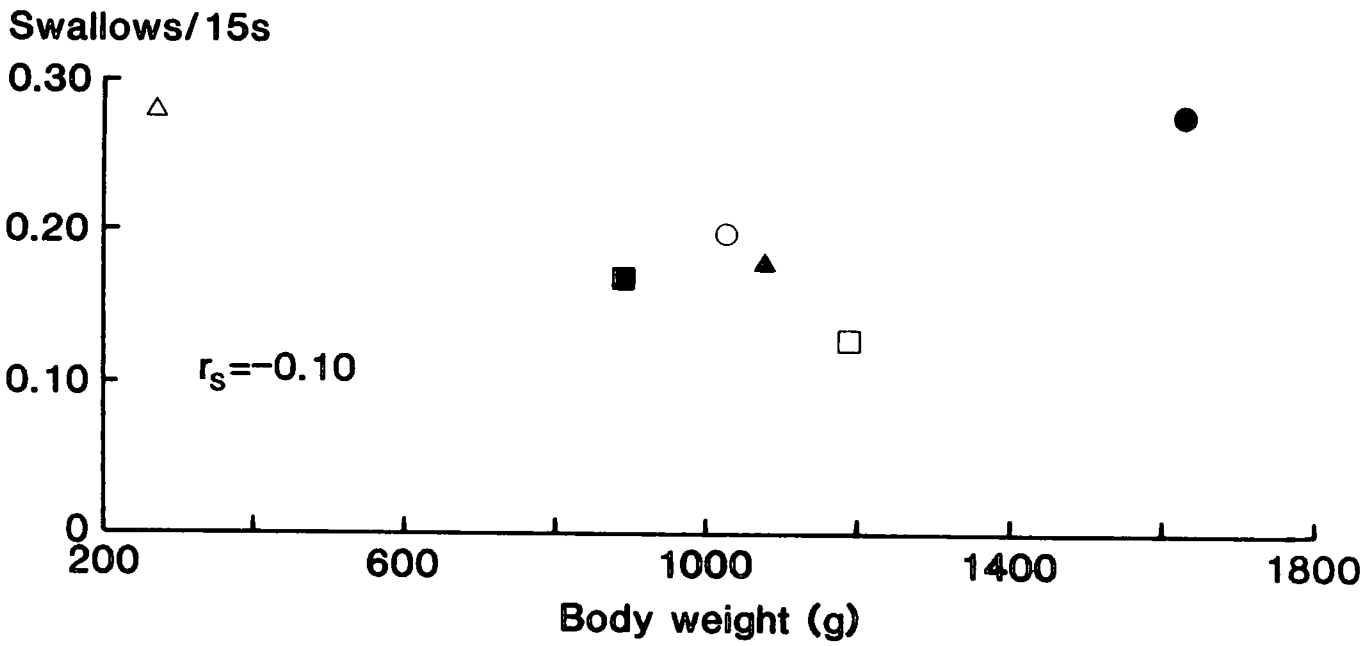

Fig. 4.3 Variation in swallowing rate with body weight

(For key to symbols see Fig. 4.1)

in support of this explanation also in relation to male and female British herring gulls. Females participated less than males in undisturbed feeding (particularly in the later stages of the feeding bout when competitive interactions were more frequent) and compensated by increased participation in disturbed feeding (Greig, et al., in press). However such an explanation does not hold for the comparison between Scandinavian and British herring gulls. Firstly, there were no differences between the races in their participation in undisturbed primary or secondary feeding, and the participation of Scandinavian herring gulls in disturbed feeding was less than that of British herring gulls. Secondly, one would expect Scandinavian herring gulls, because of their larger size and increased aggressiveness, to dominate the British birds, and achieve higher feeding success. The average rate at which British herring gulls were attacked by other herring gulls was greater than that for Scandinavian herring gulls (Table 4.8). In addition, Scandinavian herring gulls had higher average attacking rates than British herring gulls (Table 4.8). This evidence indicates a competitive advantage for Scandinavian herring gulls in intraspecific interactions. However, the overall rate at which an individual was attacked, considering attacks by both herring or great black-backed gulls, was similar for all adult herring gulls, irrespective of race (Table 4.6). This was because the proportion of attacks suffered which were initiated by great black-backed gulls varied according to species and, for herring gulls, according to race and sex, such that individuals of large body size were more likely to be attacked by great black-backed gulls than were smaller individuals (Fig.4.4). Thus, although Scandinavian herring gulls may displace British herring gulls from profitable feeding patches more often than vice versa, the former are more likely to be displaced by a great black-backed gull. Individuals of both races are therefore displaced from feeding patches with equal frequency, and hence their similar feeding success. Only 3% (n=71) of attacks made by both races of herring gull were against great black-backed gulls. Therefore, great black-backed gulls were able to use kleptoparasitism more effectively than the other gull species, and thus achieve a higher swallowing rate than either race of herring gull.

4.3.9 Effect of size within a sex

Biometric data were available for the individually marked herring gulls enabling the effect of size within a sex to be examined. Scandinavian herring gulls were not used in this analysis due to the small samples of individually marked birds available. Adult British herring gulls were divided into three size categories (small, medium and large), for both sexes, using each of two biometrics, namely head and bill length and bill depth. Head and bill length is representative of overall body size. Bill depth continues to grow after maturity (Coulson et al., 1981) and

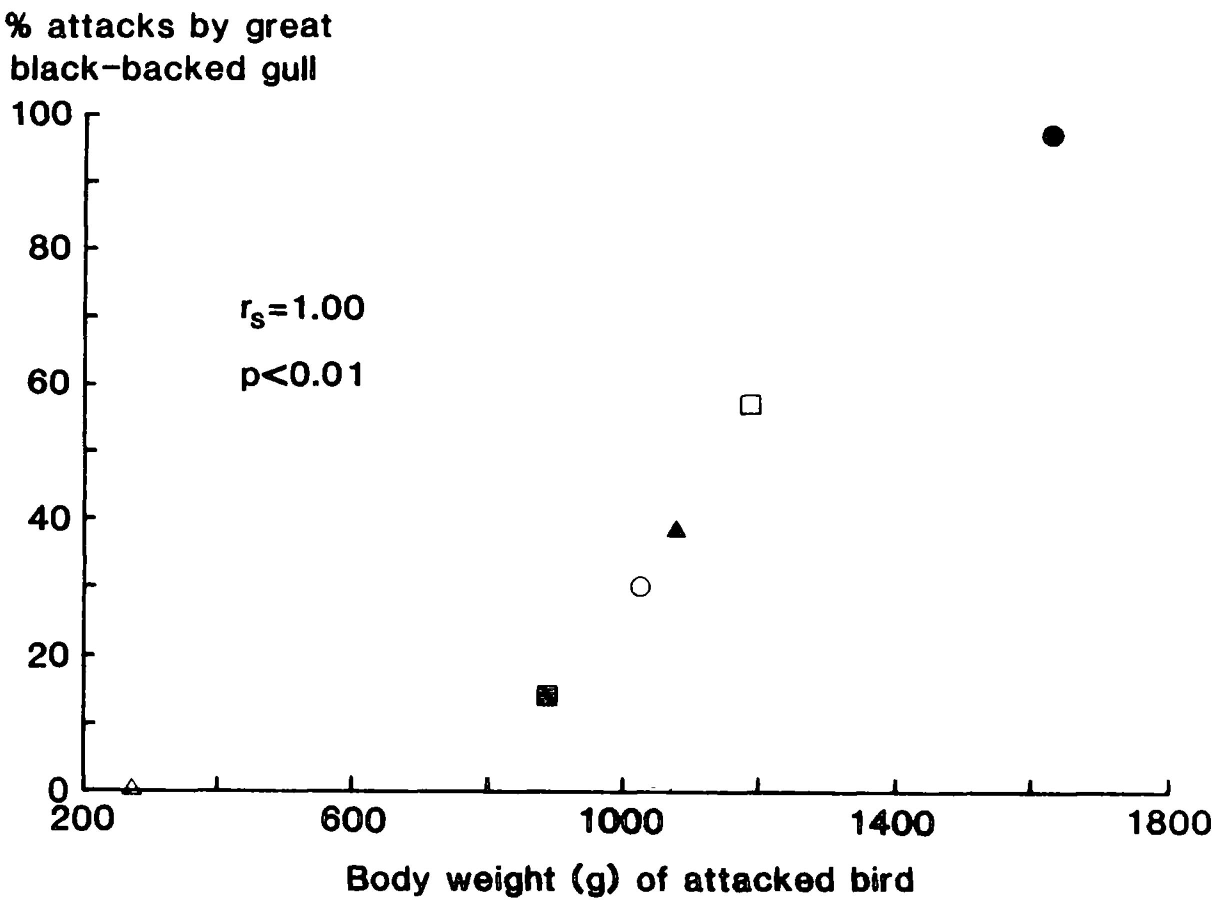

Fig. 4.4 Variation in the proportion of attacks suffered which were made by great black-backed gulls with the body weight of the attacked bird.
(For key to symbols see Fig. 4.1)

it was not significantly correlated with head and bill length in the sample of male and female herring gulls used (males; r=0.21, d.f.=49, n.s.: females; r=0.21, d.f.=61, n.s.). Adult males in the large head and bill length category had significantly higher swallow and attack rates than males in the small category (Fig.4.5, comparing large and small categories: swallow rate; t=3.31, d.f.=276, $p < 0.01$: attack rate; t=2.23, d.f.=276, $p < 0.05$). There was no difference in the rate at which different sized males were attacked by other herring gulls, but males of large head and bill lengths were attacked significantly more frequently, by great black-backed gulls, than males of small head and bill length (Fig.4.5, comparing large and small categories: t=2.74, d.f.=276, $p < 0.01$). Thus, large males were more successful, in terms of food intake, and were more aggressive, but were more likely to suffer attacks from great black-backed gulls. Males of large bill depth were also significantly more successful, in terms of swallow rate, than males with small bill depths (Fig4.6, comparing large and small categories: t= 3.12, d.f.=264, $p < 0.01$). However, there was no difference in either their attack rates or the rates at which they were attacked by great black-backed gulls. The average swallowing rate for males in each bill depth category was adjusted for differences in head and bill length using covariance analysis. Owing to the complexities of allowing for individual variation, both within and between birds, this analysis was performed on the

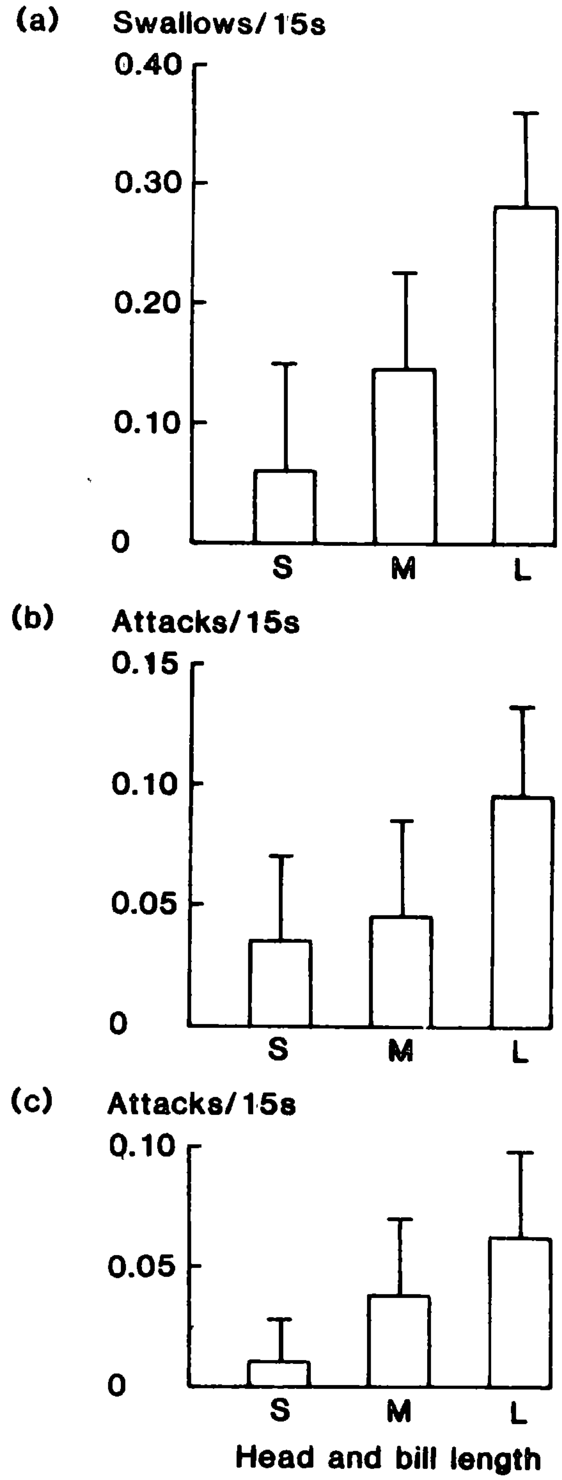

Fig. 4.5 Differences between British male herring gulls of different head and bill lengths in a) swallowing rate, b) attacking rate and c) rate of being attacked by great black-backed gulls (bars are 95% confidence limits).

S. small (< 122mm) M: medium (122-125mm)

L: large (> 125mm)

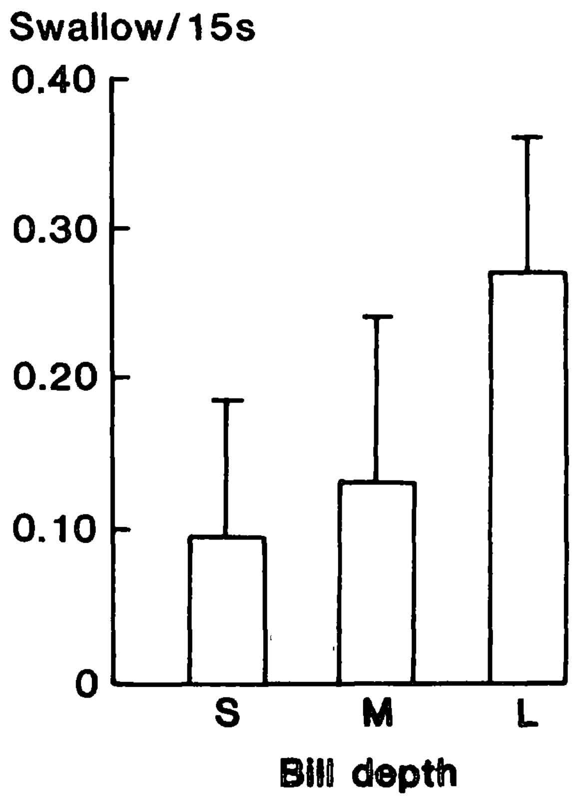

Fig. 4.6 Differences in swallowing rate between British male herring gulls of different bill depths (bars are 95% confidence limits).

S: small (< 19.0mm) M: medium (19.0-19.5mm)

L: large (> 19.5mm)

means for each bird, with a corresponding reduction in the degrees of freedom. There remained a significant trend of increased feeding success with bill depth (comparing adjusted mean swallow rate of large and small categories; $t=2.44$, d.f.$=33$, $p < 0.05$). Mean bill depth, adjusted for differences in head and bill length, is a measure of relative age, and so this relationship indicates that experience improves feeding success in adult birds. There were no size related trends in the feeding success or encounter rates of adult female herring gulls. The size related trends, in attack rate and in rate of being attacked by a great black-backed gull, present within the sample of adult male herring gulls (Fig. 4.5), are identical to those demonstrated by the interspecific comparisons described in the previous section (Figs. 4.2 & 4.4).

4.4 Discussion

Several studies have stressed the importance of refuse as a food for gulls, especially during the winter months (Spaans, 1971; Kihlman & Larsson, 1974; Mudge & Ferns, 1982). Increased food abundance resulting from increased production of refuse, in addition to that resulting from intensified commercial fishing, has been cited as a major factor in the recent population explosion of several gull species (Spaans, 1971; Harris, 1970). In this study increased numbers of great black-backed and herring gulls visited refuse tips when air temperatures were low and when wind speeds were high. There is some evidence that such conditions may be correlated with shortages of other foods. High wind speeds, through causing heavy seas, hamper fishing activities and also, through increasing water levels, decrease the availability of littoral feeding areas (Kihlman & Larsson, 1974). Studies on several wader species have shown increased use of fields as feeding sites during the winter, the implication being that the birds are unable to meet their food requirements on estuaries during this time (e.g. for oystercatchers, Haematopus ostralegus; Heppleston, 1971: for redshanks, Tringa totanus; Goss-Custard, 1969: for curlews, Numenius arquata; Townshend, 1981). Several studies have also demonstrated lower feeding rates on intertidal prey in colder weather and have related this to decreased surface activity of prey (Goss-Custard, 1977; Pienkowski, 1983a, 1983b). In addition the meat content of various intertidal molluscs decreases during the winter (Savage, 1956) as does total prey biomass (Goss-Custard, 1977) thus lowering the profitability of intertidal feeding. Prey availability on pasture also decreases at low temperature as earthworms retreat deeper into the ground (Gerard, 1967). The present study showed a clear connection between the availability of fish waste at the coast (as measured by the size of the fish catch) and numbers of great black-backed gulls at refuse tips, but not those of herring gulls. Mudge & Ferns (1982) found that great black-backed gulls used coastal feeding areas to a greater extent than did herring gulls during both summer and winter. The fact that numbers of both species at the tips increases when weather conditions are severe and when other foods are scarce or unavailable suggests that refuse may not be a preferred food. The excess of female herring gulls feeding at tips throughout the winter (Coulson et al., 1983c) suggests that tips may be less preferred feeding sites. Also, when it is cold and windy, the energetic costs of foraging are increased, due to difficulties with flight and the need to maintain body temperature (Dugan et al., 1981). In these conditions it may be advantageous to choose a foraging site which is relatively predictable.

The numbers of black-headed gulls at tips were not greatly influenced by any of the environmental variables examined. Other studies have shown that major feeding sites for black-headed gulls are fields, sewage outfalls and littoral inshore areas, with tips being relatively unimportant (Vernon, 1972; Mudge & Ferns, 1982). The increased numbers of this species at tips when winds are onshore may be due to a reduction in the availability of littoral feeding areas. The tidal cycle, which was not considered in the analysis, is also likely to be important. Differences between tips influenced black-headed gull and great black-backed gull numbers but not those of herring gulls. Horton et al. (1983), in a study of gulls feeding at some 20 tips in SE England, found that those tips with bulldozing regimes which left a large area of uncovered refuse were likely to have a lower ratio of small to large gulls. No clear pattern emerged from this study as regards tip preferences by different species but the working regime of the tip is an important factor. For herring and great black-backed gulls, although numbers may not change very much from day to day, sightings of colour ringed individuals have indicated that there is a high turnover of individuals (unpublished data). The analysis here is restricted to the average behaviour of the species or of males and females of each race of herring gull, whereas it is clear that there may be a high degree of individual variation.

Foraging at a refuse tip can involve a variety of techniques, and the three gull species investigated made different choices. Disturbed feeding required a high level of manoeuvrability at low speeds, and this favoured the smaller species. Thus, participation in disturbed feeding was related to body size, through its effect on wing loading. Scandinavian herring gulls took part in less disturbed feeding than British herring gulls and the same size-related pattern has been shown for male and female herring gulls (Greig et al., in press). In the present study, great black-backed gulls very rarely participated in disturbed feeding, their higher wing loading apparently making this type of feeding unprofitable. Comparisons between species can, in this way, indicate the limits which physical constraints such as body size place on foraging behaviour.

Clearly the probability of obtaining food is an important factor in foraging decisions. Herring gulls were found to have equal foraging success in disturbed and undisturbed primary feeding, but food gain in disturbed feeding was more variable. Their demonstrated preference for undisturbed feeding suggests that herring gulls could be making assessments of the probability of obtaining food in addition to assessing the average food gain from different feeding situations. There is experimental support for risk sensitive foraging, particularly in situations where food gain is extremely variable, so that minimising uncertainty is crucial to assure reproduction and survival (Caraco et al., 1980). A further disadvantage of disturbed feeding for gulls may be that it is energetically more costly, due to the increased time spent hovering.

Competitive ability is directly related to body size. In undisturbed feeding kleptoparasitism was frequent, and was most often and most effectively used by the largest species, the great black-backed gull. Scandinavian herring gulls and British male herring gulls used kleptoparasitism to a lesser extent, whereas female herring gulls obtained 95% of their food by independent foraging. Black-headed gulls were very rapidly excluded from competitive feeding by the larger gull species, probably as a result of avoidance rather than direct competition. Although Scandinavian herring gulls were shown to be competitively superior to British herring gulls in intraspecific interactions, they were more likely to be attacked by great black-backed gulls (Fig.4.4). It is suggested that the attacking strategy of great black-backed gulls, i.e. preferential attacking of those birds closest to their own body size, prevents Scandinavian herring gulls from achieving a higher feeding success than their British counterparts. The option of compensating by increased use of disturbed feeding, as described for the female British herring gull (Greig _et al_., in press), was not chosen by Scandinavian gulls, (in fact their participation in disturbed feeding was less than that of British herring gulls), probably because their larger body size made such feeding less profitable. The great black-backed gulls which winter in north east England are known to breed in Scandinavia (Coulson _et al_., 1984a). Thus throughout the year these great black-backed gulls remain in close contact with those herring gulls most likely to be their nearest competitors, i.e. the Scandinavian herring gulls. A study of the feeding relationships of herring and great black-backed gulls in Scandinavia, where greater overlap in size may intensify interspecific competition, might improve our understanding of the selection pressures acting on the two species throughout the year.

The size related trends in aggression, kleptoparasitism and frequency of being attacked by great black-backed gulls were also present within the group of British male herring gulls studied. The most successful males were those that were both big and old, and this indicates that experience may continue to play a part in determining foraging success in adult herring gulls. The lack of similar size-related trends, within the group of female herring gulls studied, is a reflection of their less competitive foraging strategy.

The feeding strategies which great black-backed, herring and black-headed gulls adopt at refuse tips are related to constraints placed on manoeuvrability and competitive ability by differences in body size. Differences between birds in aggressiveness and competitive ability mean that the feeding strategy and feeding success of an individual depends not only on its own competitive ability but also on the composition of the feeding flock. A more detailed analysis of the effect of flock composition on competitive interactions is presented in a subsequent paper. In order to understand the feeding ecology of these three gull species and, in particular, the role that refuse tips might play in improving overwinter survival, more information is needed on the behaviour of gulls at other feeding sites during the winter months.

5. KLEPTOPARASITISM IN HERRING AND GREAT BLACK-BACKED GULLS

5.1 Introduction

Kleptoparasitic behaviour is widespread among birds and most frequently occurs where feeding is in large flocks, at a concentrated food supply and often where large, visible food items are involved (Brockmann & Barnard, 1979). Although the term kleptoparasitism was originally introduced to describe interspecific food stealing (Rothschild & Clay, 1952), Brockmann & Barnard (1979) have suggested that there is no fundamental distinction between intra- and inter-specific kleptoparasitism, and that both may arise through individuals specialising in using the feeding information afforded by flocking. There are many examples of species which specialise in interspecific kleptoparasit ism (for a comprehensive review, see Brockmann & Barnard, 1979), but examples of individuals specialising in intraspecific food-stealing are fewer because of the need to have uniquely marked animals. Goss-Custard (1982) described the behaviour of certain individuals within a flock of oystercatchers, *Haematopus ostralegus*, which specialised in obtaining food by robbing others and which were able to achieve a higher feeding rate by this behaviour. Similar behaviour has been described for male herring gulls, *Larus argentatus*, (Greig *et al.*, in press) which, through higher attacking rates, obtained a greater proportion of food from intraspecific interactions than did female herring gulls. Barnard & Sibly (1981) distinguished two foraging strategies in flocks of captive house sparrows, Passer domesticus, which were used consistently by different individuals; copiers obtained most of their food by interaction whereas searchers found most of their food by actively foraging. The efficiency of a kleptoparasitic strategy will depend on how selective the parasite is in choosing its victims. For example, arctic skuas, Stercorarius parasiticus, preferentially attack those puffins which are carrying large, single fish (Arnason & Grant, 1978). Another factor which may affect the success of a kleptoparasitic strategy is the relative frequency of kleptoparasites in the population. Although frequency-dependent selection for kleptoparasitic behaviour may be predicted on theoretical grounds, obtaining data to test such a theory is difficult since relative success of kleptoparasitism has to be measured at different frequencies.

This study examines kleptoparasitism by herring and great black-backed gulls, L. marinus, feeding in mixed flocks at refuse tips. Use was made of a large number of uniquely marked herring gulls, colour-ringed as part of a larger study of their winter ecology. During the winter in north east England, both British herring gulls (L. argentatus argenteus) and Scandinavian herring gulls (L. argentatus argentatus) feed at tips, with Scandinavian birds forming up to 30% of the feeding flock in December and January (Coulson et al., 1984a). The race and sex of these colour-ringed herring gulls can be identified using biometrics and differences in mantle shade (Coulson et al., 1984a). Both aggression and the extent to which food is obtained by kleptoparasitism is correlated with body size (see Chapter 4). Attacks are not made at random. Herring gulls very rarely attack great black-backed gulls and large herring gulls, i.e. those of Scandinavian origin and British males, are more likely to be attacked by great black-backed gulls than are smaller herring gulls. Intraspecific herring gull encounters were more often males attacking females and Scandinavian herring gulls attacking British herring gulls than vice versa (see Chapter 4). Immature herring gulls are more aggressive than adults and rely more heavily on kleptoparasitism as a means of supplementing their less successful foraging efforts (Greig et al., 1983).

The aims of this paper are firstly, to examine the decision rules which kleptoparasitic gulls use in their selection of opponents. Secondly, a comparison of the behaviour of adult and immature herring gulls is used to look at whether successful use of kleptoparasitism depends on experience. Lastly, the possibility of frequency related effects on kleptoparasitism are examined. Since the numbers of the two species which feed at tips are variable, with those of great black-backed gulls being more variable than those of herring gulls (see Chapter 4), the effect of changes in flock composition on the behaviour of herring and great black-backed gulls could be investigated.

5.2 Methods

Data were collected on the feeding behaviour of herring and great black-backed gulls using colour video recordings made at five refuse tips in the Durham area. The recordings were made between October 1981 and February 1982 and between October 1982 and February 1983. The recordings were of undisturbed primary feeding only (see Chapter 3: Methods). Data were collected from individually colour-ringed adult herring gulls, for which sex and race was determined from their biometrics (Coulson et al., 1984a). Data were also collected from random samples of unmarked adult and immature herring gulls and adult great black-backed gulls. Immature birds were aged by plumage characteristics. Throughout this paper, birds in their first, second, third and fourth years of life are referred to as first-, second-, third- and fourth-year birds respectively. The term immature is used to refer to all these four age groups considered together. Observation periods were divided into 15-s units and the following data were recorded for each bird in each 15-s unit: (a) number of food items swallowed, (b) number and nature of encounters with other birds including the species and age of the other gulls, whether the subject initiated the attack or was the recipient, which of the birds was feeding at the time of the encounter and the outcome of the encounter. The statistical methods used in the analysis of these behavioural data followed those described by Greig et al. (in press). Counts were also made on a daily basis of the number of great black-backed and herring gulls at the tips and all sightings of colour-ringed individuals of both species were recorded.

5.3 Results

5.3.1 Kleptoparasitism

When success in an aggressive encounter is defined as the displacement of the opponent, the great majority of attacks made by both herring and great black-backed gulls were successful, with great black-backed gulls being significantly more successful than herring gulls (Table 5.1). Such a displacement involved an aggressive display which was over a few seconds. Escalations of contests were very rarely observed. This suggests that the great majority of encounters were asymmetric and that attackers were good at assessing the competitive ability of their potential victims (Maynard Smith & Parker, 1976). The distribution of attacks made by great black-backed gulls against conspecifics and against herring gulls, when compared with the relative proportions of the two species present, show that great black-backed gulls attacked significantly more conspecifics than expected, assuming attacks were made at random with respect to the species of the opponent (Table 5.2). Herring gulls very rarely attacked great black-backed gulls, and in 6 out of the 7 instances when such an attack was made, the herring gull was unsuccessful in displacing the great black-

Table 5.1 Proportion of attacks which were successful in terms of displacing the opponent, considered for herring gulls and great black-backed gulls.

Attacker	No. attacks won	No. attacks lost	% won
Great black-backed gull	329	4	99
Herring gull	296	29	91

$\chi^2_1 = 19.0$, $p < 0.001$

Table 5.2 Number of attacks made by great black-backed gulls against conspecifics and against herring gulls, compared with expected numbers assuming attacks were made at random with respect to the species of the opponent. The expected values are calculated from the average species composition at a tip, of 8 % great black-backed gulls.

	No. attacks against herring gulls	No. attacks against great black-backed gulls	% attacks against conspecifics
Observed	148	32	18
Expected	166	14	8

Comparing observed and expected values; $\chi^2_1 = 25.1$, $p < 0.001$

backed gull. Thus, most herring gulls were able to recognise great black-backed gulls as unprofitable opponents. In inter-specific encounters large differences in body size and appearance act as clear signals of competitive ability. The difference in body size between the sexes and races of herring gull may act as a signal of relative dominance status, and thus give rise to the pattern of males attacking females and Scandinavian herring gulls attacking British herring gulls. Thus the decision as to who to attack may involve an 'attack only if you are larger than the potential victim' rule.

Feeding rates of individuals of both species who made one or more displacement attack were compared with those of individuals who were not observed to attack (Table 5.3). For adult herring gulls only, the sexes and races are considered separately. For adult British male herring gulls and herring gulls in their third or fourth year, aggression was a successful way of obtaining food (Table 5.3). Great black-backed gull, adult British female herring gulls and Scandinavian herring gulls of both sexes did not improve their feeding rates by attacking (Table 5.3). In contrast aggressive herring gulls in their first and second year of life had significantly lower feeding rates than those who did not attack (Table 5.3). The proportion of attacks which led to food gain was approximately a third for adult male and female herring gulls of both races and for great black-backed gulls (Table 5.4). Immature herring gulls had a

Table 5.4 Proportion of attacks which led to food gain considered for herring gulls of different age, sex and race and for adult great black-backed gulls.

	Total no. attacks made	No. attacks leading to food gain	% attacks leading to food gain
1st and 2nd year herring gulls	105	13	12
3rd and 4th year herring gulls	38	7	18
Adult British male herring gulls	19	9	47
Adult British female herring gulls	9	2	22
Adult Scandinavian male herring gulls	12	4	33
Adult Scandinavian female herring gulls	6	3	50
Adult great black-backed gulls	185	60	32

Table 5.3 Mean swallowing rates of herring gulls and great black-backed gulls which made one or more displacement attacks compared with the mean swallowing rates of individuals of both species which did not attack.

	Swallowing rate of attacker			Swallowing rate of non-attacker				
	n	mean	SE	n	mean	SE	t	p
1st and 2nd year herring gull	369	0.035	0.014	442	0.120	0.026	2.99	< 0.01
3rd and 4th year herring gull	195	0.181	0.033	314	0.086	0.024	2.36	< 0.05
Adult British male herring gull	150	0.256	0.047	241	0.140	0.042	1.86	n.s.
Adult British female herring gull	87	0.166	0.097	279	0.166	0.044		n.s.
Adult Scandinavian male herring gull	53	0.105	0.048	18	0.192	0.094		n.s.
Adult Scandinavian female herring gull	22	0.229	0.103	73	0.186	0.056		n.s.
Adult Great black-backed gull	557	0.304	0.049	343	0.231	0.048	1.06	n.s.

significantly lower attack success of 14% as compared with 39% for adult herring gulls (χ^2_1 = 12.2, p < 0.001). Therefore, despite success in displacement in over 90% of cases, the attacking bird only achieved food gain from one attack in three, and one attack in six in the case of herring gulls in their first and second years. This raises the question 'does the attacking bird make an assessment of the profitability of an attack, and if so what criteria does it use?'. Two factors, which might influence the frequency with which individuals were attacked, were investigated; a) prior swallowing by 'victim', b) prior attacking by 'victim'. It was thought that swallowing a food item might attract attacks from neighbouring gulls, whereas attacking could be a signal of dominance and as such deter attacks by neighbouring gulls. The proportion of victims which made at least one attack or swallowed at least one food item in the 30s prior to being attacked was compared with an expected value derived from the observed proportions of birds attacking or swallowing within a 15s observation period. Three types of encounter were examined: a) great black-backed gull attacks great black-backed gull, b) great black-backed gull attacks herring gull, c) herring gull attacks herring gull, the latter being divided into adult-adult, adult-immature, and immature-immature encounters. Conspecific attacks in great black-backed gulls were at random with respect to the prior behaviour of the object of the attack (Table 5.5). When great black-backed gulls attacked

Table 5.5 Prior behaviour of victims of attacks by great black-backed gulls, with respect to swallowing or attacking. Observed values are compared with expected values, assuming attacks were at random with respect to the prior behaviour of the victim.

Encounter	Behaviour of attacked bird in 30s prior to attack	Observed			Expected			Significance
		n	mean	SE	n	mean[a]	SE[b]	
Great black-backed gull attacks conspecific	Proportion swallowing $\geq$ 1 food item	46	0.35	0.07	1098	0.34	0.02	n.s.
	Proportion making $\geq$ 1 attack	46	0.52	0.07	1098	0.42	0.02	n.s.
Great black-backed gull attacks herring gull	Proportion swallowing $\geq$ 1 food item	79	0.28	0.05	2267	0.23	0.01	n.s.
	Proportion making $\geq$ 1 attack	79	0.42	0.06	2267	0.12	0.01	$t=5.30$, $p < 0.001$

[a] mean = $2p - p^2$ where p is the proportion of birds making $\geq$ 1 attack or obtaining $\geq$ 1 food item in 15s

[b] SE = $2(1 - p)$ SE_p where SE_p is the standard error of p (Aebischer, pers. comm.)

herring gulls, their victims were three and a half times more likely to have attacked in the 30s before the attack (Table 5.5). Far from being deterred by aggression, great black-backed gulls therefore showed a marked positive response to aggression in herring gulls. This selection of aggressive birds would explain the significantly higher attack rates against male rather than female herring gulls and the similar size (and aggression) related trends in the rates at which Scandinavian and British herring gulls of both sexes are attacked (see Chapter 4). Since great black-backed gulls are dominant to herring gulls, one might not expect them to be intimidated by aggressive herring gulls. However, conspecific herring gull encounters showed a similar positive response by adults to aggression when attacking other adult herring gulls and again no apparent response to prior swallowing on the part of a potential victim (Table 5.6). This result is more surprising, and, together with the evidence from great black-backed gull attacks, indicates that aggression acted as a cue for attack. Herring gulls in their third and fourth years of life showed similar trends to those of adults, with a positive response to aggression and not to swallowing when attacking adults (Table 5.7). First and second year birds had a significant positive response to prior swallowing by adults and no response to aggression (Table 5.8). Attacks against immature herring gulls were at random with respect to their prior attacking or swallowing rates, for all

Table 5.6 Prior behaviour of victim of adult herring gull attacks, with respect to swallowing or attacking. Observed values are compared with expected values assuming attacks were at random with respect to the prior behaviour of the victim.

Encounter	Behaviour of attacked bird in 30s prior to attack	Observed			Expected[a]			Significance
		n	mean	SE	n	mean	SE	
Adult herring gull attacks adult herring gull	Proportion swallowing ⩾ 1 food item	55	0.35	0.06	947	0.29	0.02	n.s.
	Proportion making ⩾ 1 attack	55	0.35	0.06	947	0.13	0.02	$t=3.20$, $p < 0.01$
Adult herring gull attacks immature* herring gull	Proportion swallowing ⩾ 1 food item	40	0.20	0.06	1320	0.18	0.02	n.s.
	Proportion making ⩾ 1 attack	40	0.28	0.07	1320	0.29	0.02	n.s.

* 1-4 years

[a] for derivation of expected values, see Table 5.5

Table 5.7 Prior behaviour of victims of attacks by third and fourth year herring gulls, with respect to swallowing and attacking. Observed values are compared with expected values assuming attacks were at random with respect to the prior behaviour of the victim.

Encounter	Behaviour of attacked bird in 30s prior to attack	Observed			Expected[a]			Significance
		n	mean	SE	n	mean	SE	
Third or fourth year herring gull attacks adult herring gull	Proportion swallowing ≥ 1 food item	10	0.30	0.15	947	0.29	0.02	n.s.
	Proportion making ≥ 1 attack	10	0.40	0.16	947	0.13	0.02	t=1.71, n.s.
Third or fourth year herring gull attacks immature* herring gull	Proportion swallowing ≥ 1 food item	4	0.50	0.25	1320	0.18	0.02	n.s.
	Proportion making ≥ 1 attack	4	0	-	1320	0.29	0.02	n.s.

* 1-4 years

[a] for derivation of expected values, see Table 5.5

Table 5.8 Prior behaviour of victims of attacks by first and second year herring gulls, with respect to swallowing and attacking. Observed values are compared with expected values assuming attacks were at random with respect to the prior behaviour of the victim.

Encounter	Behaviour of attacked bird in 30s prior to attack	Observed			Expected[a]			Significance
		n	mean	SE	n	mean	SE	
First or second year herring gull attacks adult herring gull	Proportion swallowing ⩾ 1 food item	36	0.47	0.08	947	0.29	0.02	$t=2.13$, $p < 0.05$
	Proportion making ⩾ 1 attack	36	0.22	0.07	947	0.13	0.07	n.s.
First or second year herring gull attacks immature* herring gull	Proportion swallowing ⩾ 1 food item	47	0.13	0.05	1320	0.18	0.02	n.s.
	Proportion making ⩾ 1 attack	47	0.30	0.07	1320	0.29	0.02	n.s.

* 1-4 years

[a] for derivation of expected values, see Table 5.5

attackers irrespective of age (Tables 5.6, 5.7 & 5.8). Thus, herring gulls of three years and older preferentially attacked adults who had themselves made an attack within the previous 30 seconds. In contrast, first and second years preferentially attacked adults who had swallowed a food item within the previous 30 seconds and they did not use attacking by adults as a cue for attack. The behaviour of great black-backed gulls and of herring gulls of 3 years and older was consistent with an attack rule 'attack only if you are bigger than the potential victim, attack aggressive birds preferentially'. Aggression was therefore associated with the presence of food, and this resulted in one attack in three leading to food gain. The possible origins of such decision rules are discussed later. The response of immature gulls was to swallowing (and not attacking) by potential victims, and this was a less successful strategy resulting in food gain from one attack in six. Swallowing clearly is associated with the presence of food, but making an attack after a potential victim has swallowed may be too late. Also, even if immature gulls do obtain profitable feeding patches by attacking, they may be unable to extract edible items from the refuse. The lack of response to aggression may be due to first and second year birds being inhibited from attacking aggressive adults. The distribution of conspecific herring gull attacks, with respect to the ages of both attacker and attacked, indicates that younger birds attacked proportionally less adults than did older herring gulls (Table 5.9).

5.3.2 Changes in the composition of the feeding flock

As the proportion of great black-backed gulls in the feeding flock changed, so did the flock composition with respect to sex-ratios of both species and also with respect to the relative numbers of British and Scandinavian herring gulls present. Evidence from sightings of colour-ringed birds of known sex indicated that the sex-ratio of both species was more male biased when the proportion of great black-backed gulls present was high (Fig. 5.1; Table5.10). Also the proportion of herring gulls which were of Scandinavian origin was positively correlated with the proportion of great black-backed gulls (Fig. 5.1). In addition, the average bill depth of the male herring gulls present when the proportion of great black-backed gulls was 5% or over was greater than that when great black-backed gulls were few (Table 5.11). There was no evidence of a change in the average head and bill length. Therefore the male herring gulls present at higher levels of great black-backed gull abundance were, on average, older. Overall, there was a shift in flock composition towards the larger (and in the case of the male herring gull, older) individuals of both species, when the proportion of great black-backed gulls was over 5%. These changes in flock composition are summarised in Figure 5.2.

Table 5.9 Distribution of herring gull attacks with respect to the age of both the attacking and the attacked bird.

		Age of attacked herring gull					
		1 yr	2 yr	3 yr	4 yr	Adult	% attacks against adult herring gulls
Age of attacking herring gull	Adult	3	1	4	0	38	83
	3-4 yr	4	4	2	2	22	65
	1-2 yr	21	9	15	2	66	58

Comparing the adult, 3-4 yr and 1-2 yr age groups with respect to the proportion of attacks made against adults: $\chi^2_2 = 8.49$, $p < 0.05$.

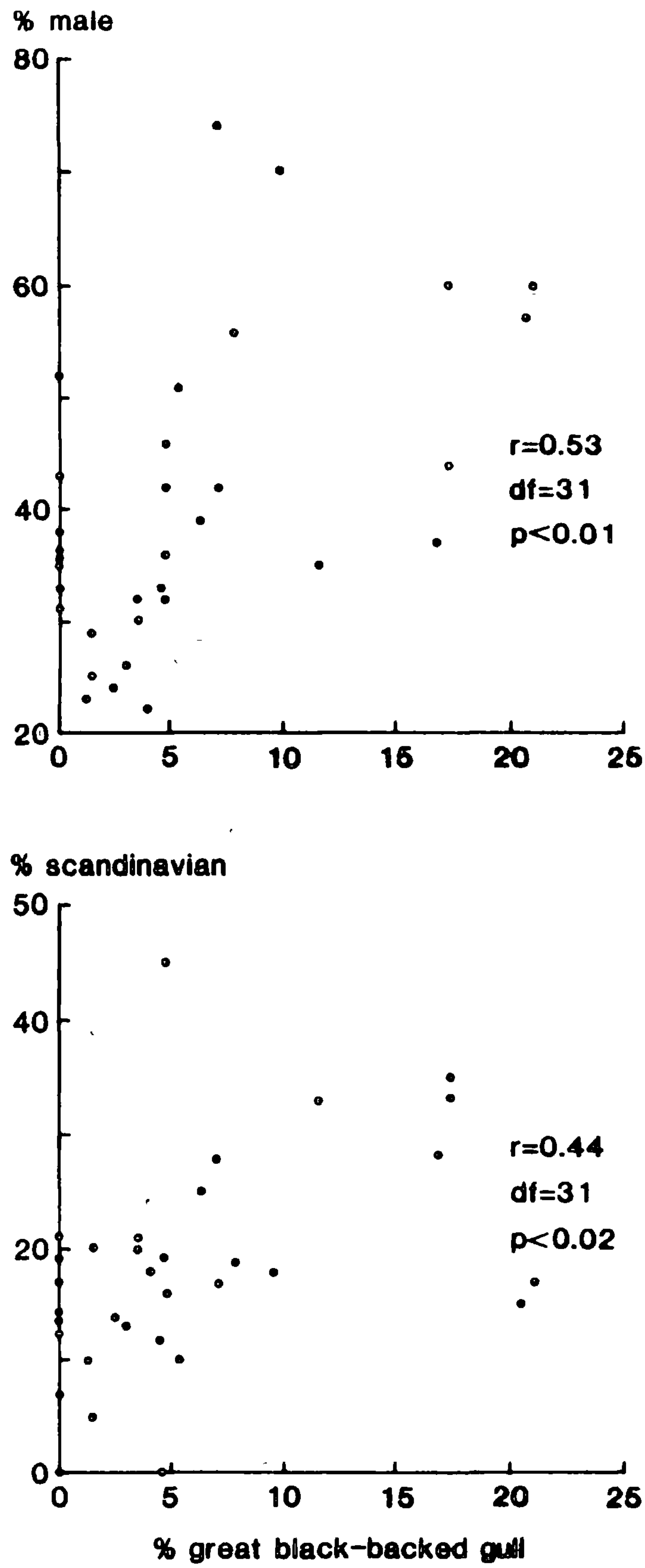

Fig. 5.1 Relationship between a) the sex-ratio of British herring gulls, and b) the proportion of herring gulls which were of the Scandinavian race, and the proportion of great black-backed gulls present.

Table 5.10 Number of sightings of male and female adult great black-backed gulls at different levels of great black-backed gull abundance.

	Proportion of great black-backed gulls		
	< 5%	5–15%	> 15%
	No. sightings	No. sightings	No sightings
Male	4	11	15
Female	13	14	14
% female	76	56	48

$\chi^2_2 = 3.54$, n.s.

Table 5.11 Bill depth and head and bill length of British male herring gulls at different great black-backed gull abundance levels.

		Proportion of great black-backed gulls		
		< 5%	5–15%	> 15%
Bill depth	n	145	107	60
	mean	19.38	19.62	19.57
	SE	0.05	0.06	0.08
Head and bill length	n	145	108	59
	mean	124.4	124.0	123.7
	SE	0.3	0.3	0.5

Significance	Bill depth	Head and bill length
< 5% GBB compared with 5–15% GBB	$t=3.03$, $p < 0.01$	$t=0.94$, n.s.
< 5% GBB compared with > 15% GBB	$t=2.04$, $p < 0.05$	$t=1.20$, n.s.

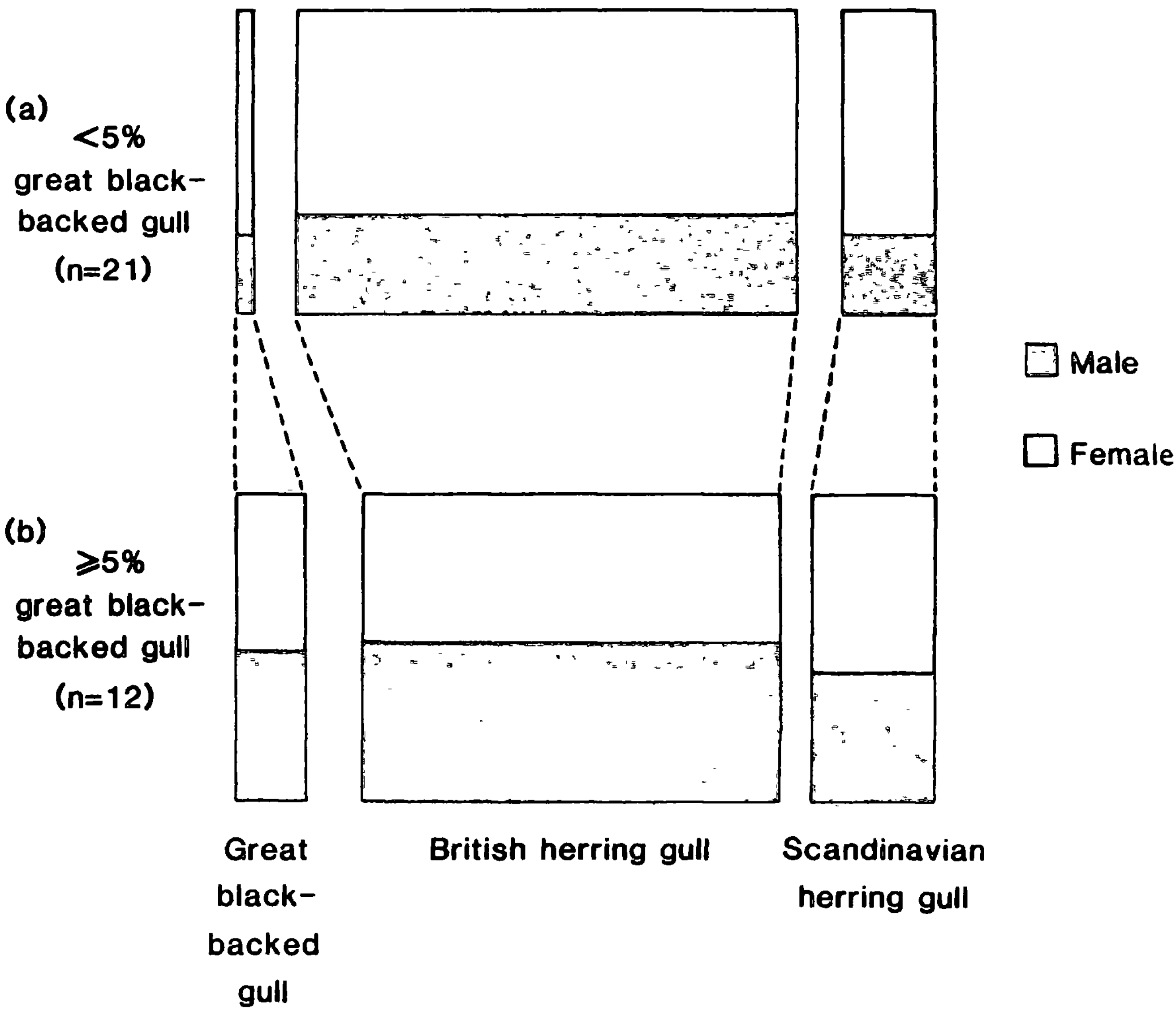

Fig. 5.2 Changes in flock composition associated with a change in the proportion of great black-backed gulls present.

5.3.3 Competitive interactions between herring and great black-backed gulls

In view of the kleptoparasitic feeding strategy used by great black-backed gulls and to a lesser extent by herring gulls (depending on their race and sex), it might be expected that variability in the relative proportions of the two species feeding together would have an effect on the performance of, or feeding strategies used by individuals of both species, and for herring gulls, of both races and both sexes. Since the incidence of competitive interactions between great black-backed gulls and herring gulls depends on their relative proportions, the percentage of great black-backed gulls in the feeding flock was used to define three categories of great black-backed gull abundance: a) high (> 15%), b) medium (5-15%) and c) low (< 5%). The behaviour of male and female British herring gulls, and of great black-backed gulls under these different conditions are described in the following sections. It was not possible to make a similar comparison of the two races of herring gulls due to small sample sizes for the Scandinavian race.

5.3.4 Great black-backed gull abundance and feeding behaviour of male and female adult herring gulls

Greig et al. (in press) described the changes in the feeding behaviour of male and female adult herring gulls which took place throughout the course of an undisturbed primary feeding bout. It is necessary to summarise the main points in order to give a background to the analysis of the effect of varying great black-backed gull abundance. Swallowing rates of the two sexes were comparable in the first ten minutes of the feeding bout, but thereafter female swallowing rate declined significantly whereas that of males was sustained. The later stages of the feeding bout were also characterised by increased levels of aggression in males. Thus as the feeding bout progressed, male dominance led to a lower feeding performance in females.

Feeding rates for male and female adult herring gulls under conditions of high, medium and low great black-backed gull abundance, and divided between the first ten minutes of the feeding bout and later, are shown in Figure 5.3. The proportion of great black-backed gulls present exceeded 15% on only four days out of the 33 on which observations were made. Consequently the sample of colour-ringed herring gulls observed under these conditions was relatively small. When the proportion of great black-backed gulls present was high, scramble competition seemed to operate with female herring gulls having a slightly higher swallowing rate than males ($t=2.19$, $p < 0.05$) and the encounter rates, both attacking and being attacked, of the two sexes being similar. Only 7% (n=60) of observations on herring gulls of both sexes were recorded after ten minutes from the start of feeding. Of 23 feeding bouts, 74% lasted for longer than ten minutes and so this lack of observations was not due to

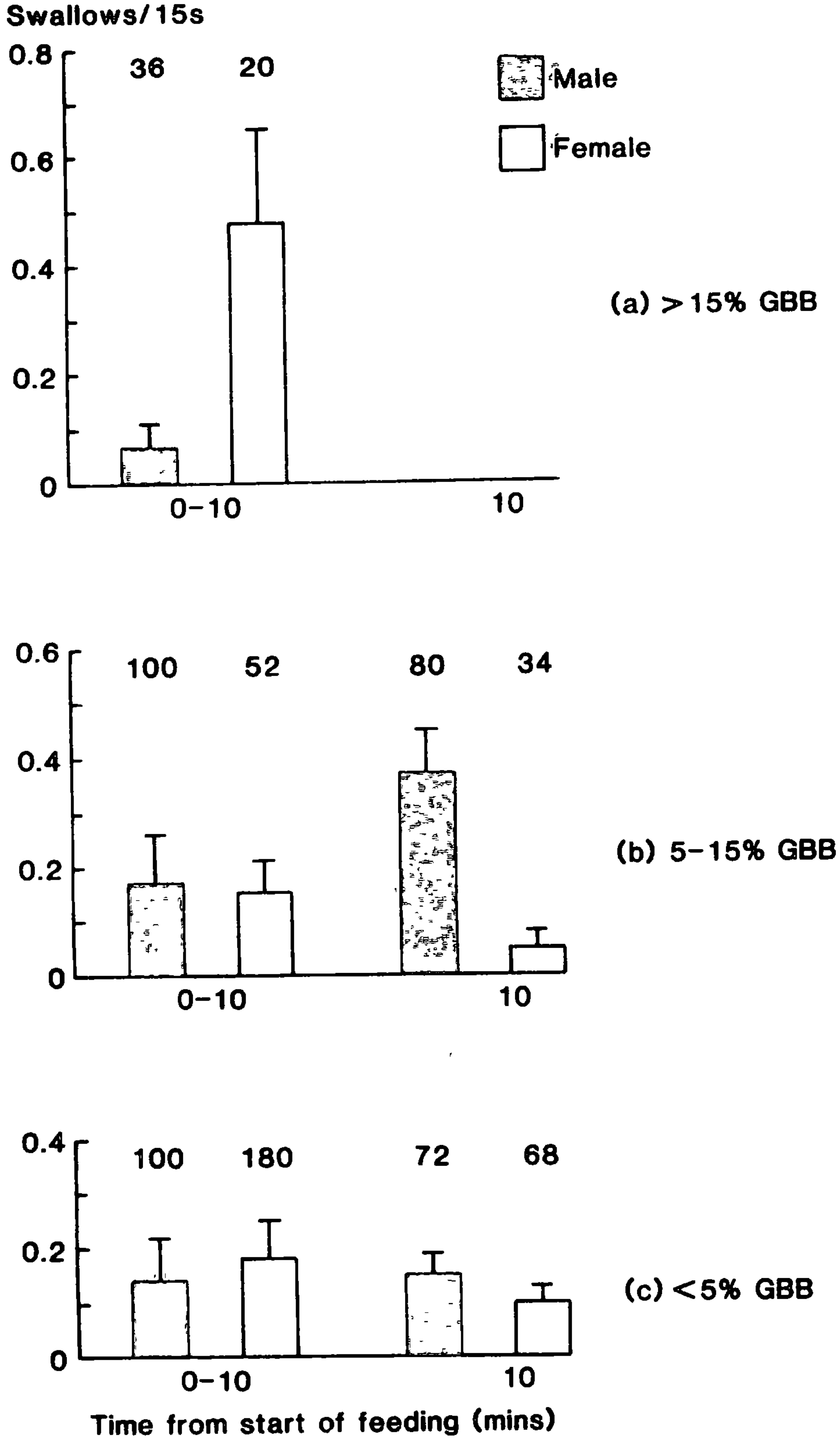

Fig. 5.3 Changes in feeding rates of adult male and female herring gulls throughout the feeding bout, considered separately for three levels of great black-backed gull abundance (bars are 1 SE, sample sizes shown at top of figure).

GBB: great black-backed gull

a lack of longer feeding bouts. It was more probably a result of a marked decline in herring gull numbers. That some herring gulls were responding to high great black-backed gull abundance by giving up and leaving the feeding area is further supported by sample counts of the feeding birds during the course of a number of feeding bouts. The percentage of great black-backed gulls increased throughout the feeding bout (whilst the total number of birds feeding tended to decrease) and reached 29% after 10 minutes compared with an average of 18% great black-backed gulls present at the tip. Sightings of colour-ringed herring gulls gave no evidence of a change in sex-ratio, indicating that the sexes responded in the same way.

When great black-backed gulls comprised between 5 and 15% of the feeding flock, the feeding behaviour of male and female herring gulls was different in several respects. Although there were no differences in swallowing rate between the sexes in the first ten minutes of feeding, suggesting scramble competition for food, males achieved a significantly higher swallowing rate than females ($t=3.87$, $p < 0.01$), later in the feeding bout. When great black-backed gulls were relatively scarce (< 5%), the swallowing rates of the sexes showed a similar pattern, that of males increasing and that of females decreasing as the feeding bout progressed. However, the female rate only declined to 65% of that of the male, and none of the differences were significant. Therefore when few great black-backed gulls were present, dominance by male herring gulls over females was not expressed. One explanation for this effect is that great black-backed gulls are simply acting as extra male herring gulls, and as such their presence enhances male dominance. However, the average proportion of great black-backed gulls present in the medium abundance category was 8% and it seems surprising that relatively few birds could have so great an effect. In addition, great black-backed gulls attacked male herring gulls more than females (see Chapter 4), and on this basis one might expect their presence to depress male dominance, as was the case when the proportion of great black-backed gulls was greater than 15%. The changes in flock composition which accompanied an increase in the proportion of great black-backed gulls present have been described (Fig.5.2). The proportion of males amongst the British herring gulls and the proportion of herring gulls which were of Scandinavian origin were positively correlated with the proportion of great black-backed gulls (Fig.5.1). Since aggression is related to size, this change in flock composition amounts to an increase in aggressiveness and in kleptoparasitism. Therefore, when great black-backed gulls were scarce, so were kleptoparasitic herring gulls; their effect on female herring gulls was small, and no differences in feeding performance between the sexes was found. As the proportion of great black-backed gulls increased, so did the proportion of kleptoparasites, and so the feeding performance of their victims (the female herring gulls) was reduced. When the proportion of great black-backed gulls was more than 15%, the kleptoparasitic herring gulls (mostly British male herring gulls) were at a disadvantage and responded by leaving the feeding area.

However this does not explain why male herring gulls had higher feeding success in the later stages of the feeding bout when the proportion of great black-backed gulls present was between 5 and 15% than when the proportion was less than 5% (Fig. 5.3). The explanation may lie in the increased average age of male herring gulls which fed at tips at medium and high levels of great black-backed abundance. If age and therefore experience continue to improve feeding success in adult life, then this might explain the higher feeding rates of male herring gulls in this situation.

5.3.5 Great black-backed gull abundance and feeding behaviour of adult great black-backed gulls

Feeding rates for adult great black-backed gulls under conditions of high, medium and low great black-backed abundance and for the first ten minutes of the feeding bout and later are shown in Fig.5.4. For all levels of great black-backed gull abundance, swallowing rate declined throughout the feeding bout ($t=2.70$, d.f.$=898$, $p < 0.01$). This contrasts with the behaviour of male herring gulls, described in the previous section, which were able to sustain or even increase their swallowing rate, through

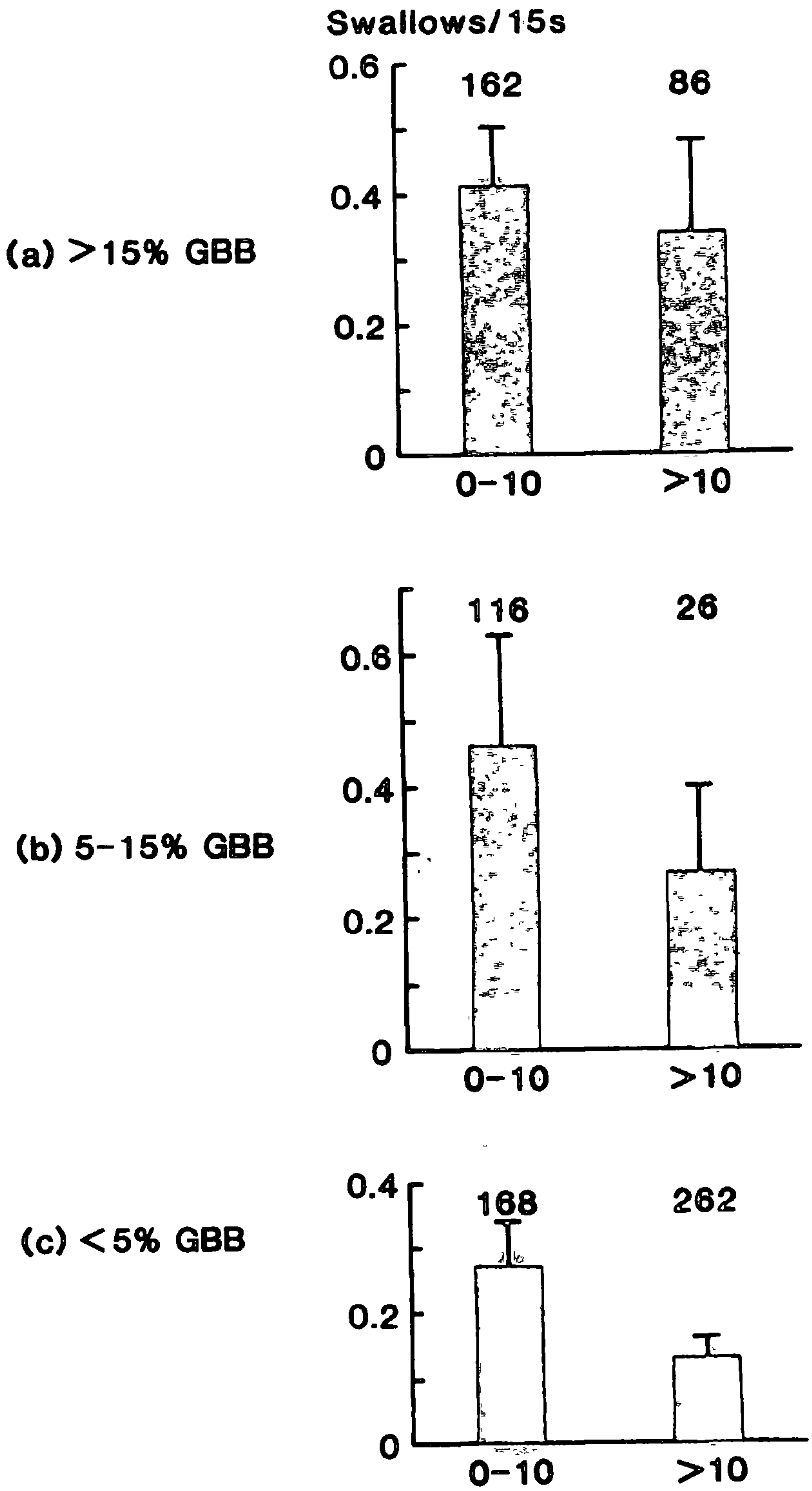

Fig. 5.4 Changes in feeding rates of adult great black-backed gulls throughout the feeding bout, considered separately for three levels of great black-backed gull abundance (bars are 1 SE, sample sizes shown at top of figure).

GBB: great black-backed gull

increased use of kleptoparasitism. However the swallowing rates of male herring and great black-backed gulls in the later stages of the feeding bout were comparable (cf. values in Figs 5.3 & 5.4). It therefore seems likely that the decline in feeding success of great black-backed gulls throughout the feeding bout was due to food or targets for attack becoming limiting. Abundance had a positive effect on swallowing rate for both time periods. Combining the two time periods, swallowing rate at high abundance was significantly greater than at low abundance (t=2.78, d.f.=676, $p < 0.01$) and not significantly different from that at medium abundance. In addition when great black-backed gulls were scarce, 48% (n=108) of their food was obtained by kleptoparasitism compared with 69% (n=81) and 61% (n=128) at medium and high levels of abundance respectively (Low vs. Med. + High $\chi^2_1 = 7.41$, $p < 0.01$). The distribution of observations throughout the feeding bout indicates that at low abundance (i.e. low profitability) 62% (n=430) of observations were made after the first ten minutes compared with 18% (n=142) at medium abundance and 35% (n=248) at high abundance (combining high and medium categories and comparing with low: $\chi^2_1 = 84.2$, $p < 0.001$). This suggests that when great black-backed gulls are relatively scarce, they compensate for a low swallowing rate by feeding longer.

What is the basis for the positive effect of the proportion of great black-backed gulls present on their average swallowing rate? There were no significant differences in total encounter rates between the three abundance categories. However the way in which attacks were distributed between herring and great black-backed gulls did change, such that at high levels of great black-backed abundance, 35% of attacks were against conspecifics compared with 15% and 13% at medium and low levels respectively (Table 5.12). In addition, when great black-backed gulls were scarce, 52% of their attacks were directed against immature herring gulls, compared with 23% and 26% at medium and high abundance levels respectively (Table 5.12). An examination of success in attack (defined as the proportion of attacks which resulted in food gain) shows that success depended on the nature of the opponent (Table 5.13). There was a trend of increasing success from immature herring gull, adult herring gull, immature great black-backed gull to adult great black-backed gull and this was a reflection of the differences in average swallowing rate between these four groups. Thus low feeding performance when great black-backs are scarce can be explained in terms of a less successful attacking strategy by great black-backed gulls, i.e. one of concentrating attacks on immature herring gulls.

As the proportion of great black-backed gulls increased, intraspecific interactions increased, and whilst a kleptoparasitic strategy might continue to benefit dominant individuals, one might expect that there would be a level of great black-backed gull abundance where such a

Table 5.12 Distribution of attacks by great black-backed gulls by age and species of opponent in categories of different great black-backed gull abundance.

	Proportion of great black-backed gulls					
	< 5%		5–15%		> 15%	
Opponent	No. attacks	col %	No. attacks	col %	No. attacks	col %
Immature HG	56	52	7	23	11	26
Adult HG	38	36	19	63	17	39
Immature GBB	5	5	0	0	1	2
Adult GBB	8	7	4	13	14	33

HG: herring gull

GBB: great black-backed gull

Table 5.13 The proportion of attacks made by adult great black-backed gulls which resulted in food gain separated into attacks on immature and on adult herring and great black-backed gulls.

Opponent	Immature HG	Adult HG	Immature GBB	Adult GBB
No. attacks observed	78	75	6	26
% attacks with good gain	24	35	33	50

χ^2 test for linear trend in proportions: $\chi^2_1 = 5.89$, $p < 0.05$

HG: herring gull

GBB: great black-backed gull

strategy was no longer profitable for subordinate individuals. Although the proportion of food obtained by attack and the average swallowing rate both showed a decline at high levels of great black-backed abundance, in neither case was the difference significant. Thus, over the range of proportions of great black-backed gulls recorded in this study, kleptoparasitism remained a viable way of obtaining food.

5.4 Discussion

Kleptoparasitism in the Laridae is probably the result of birds capitalising on feeding opportunities presented in high density, mixed species flocks at a rich food source (Brockmann & Barnard, 1979). As such, one might not expect such specialised behaviour in the choice of victim as that shown, for example, by the arctic skua, for which kleptoparasitism is more a way of life. Both great black-backed and herring gulls preferentially attacked herring gulls which had made an attack within the previous 30 seconds. Thus both species associated aggression with the presence of food. Aggression indicates that a feeding bird is likely to have something worth defending. This response to aggression is often seen at refuse tips when any slightly protracted dispute over a food item rapidly attracts a large number of gulls. Attacks, apparently based on this decision rule, led to food gain in approximately a third of cases, for both herring and great black-backed gulls. This response to aggression provides an explanation for the greater frequency with which large herring gulls (British males and Scandinavians) are attacked by great black-backed gulls. Immature herring gulls, in contrast, did not selectively attack aggressive adult herring gulls. Immature birds responded to swallowing by adults and this was a less successful attacking strategy, leading to food gain from only one attack in six. This may have been a result of younger herring gulls being inhibited from attacking aggressive adults. Alternatively, it may be that first and second year herring gulls associated swallowing in adults with being fed by them and that aggression towards such adults resulted from a frustration of this expectation. When great black-backed gulls were scarce, they had an apparently non-optimal strategy of concentrating attacks on immature herring gulls. Immature herring gulls are more aggressive than adults (Verbeek, 1977a, 1977b; Greig et al., 1983), and the low proportion of aggressive adult herring gulls (i.e. British males and Scandinavians) and of great black-backed gulls under these conditions could explain the observed distribution of attacks.

When weather conditions were severe and other foods scarce, the numbers of both herring and great black-backed gulls feeding at tips increased (see Chapter 4). The increase in great black-backed gull numbers was proportionally greater than that for herring gulls and so the proportion of great black-backed gulls present was higher under such conditions. Changes in the proportion of great black-backed gulls were found to be associated with other changes in flock composition. When the proportion of great black-backed gulls at the tips was 5% or over, the sex-ratio of both great black-backed and herring gulls was male biased. In addition the increased bill depth of the male herring gulls present suggests that they were, on average, older. The proportion of Scandinavian herring gulls present was also correlated with that of great black-backed gulls. Thus, in severe weather it was particularly the larger (and in the case of the male herring gull, older) individuals which came into the tips in greater numbers. This suggests that under favourable environmental conditions, there may be some separation of the sexes, with more males of both species (and especially older male herring gulls) feeding at preferred sites on the coast, and more females feeding inland at refuse tips. In a study of herring gulls during the breeding season, Sibly & McCleery (1983a, 1983b) found no sex related differences in food preferences, but they regarded fish, either obtained by direct capture or by scavenging at trawlers and at fish quays, as a minor food source, and therefore had no information on individuals using such sites. Niebuhr (1983) and Belopol'skii (1961) both reported more females feeding on intertidal foods in the breeding season. In the latter study, male herring gulls ate correspondingly more fish but refuse was not used by either sex. During the incubation period, and to a lesser extent during chick-rearing, it is necessary for the two members of the pair to adopt complementary foraging patterns, since foods vary in their temporal availability (Sibly & McCleery, 1983b). Also there may be nutritional constraints, such as calcium deficiency in females incurred by egg production, which lead to particular foraging patterns (Niebuhr, 1983). In winter such constraints on foraging behaviour are absent, and so foraging patterns may be quite different. Also, outside the breeding season, the time available for foraging is increased, although this is to some extent offset by the decrease in daylight hours. Detailed information on the sex ratio of gulls using feeding sites other than refuse tips during the winter months is lacking, but of 27 herring gulls caught from the back of a fishing boat, 19 were males (Monaghan, unpublished data) thus supporting the idea of some feeding separation between the sexes in the winter months.

The extent to which herring gulls, and particularly the smaller female herring gull, were disadvantaged during competitive feeding depended on the proportions of great black-backed gulls, male herring gulls and Scandinavian herring gulls which were present. All these three proportions were positively intercorrelated. For much of the winter, there was an excess of female herring gulls at tips and the proportion of great black-backed gulls present was low (< 5%). Under these conditions there was no difference in feeding success between the sexes or races of herring gulls, but great black-backed gulls achieved a higher feeding success. When the weather was more severe the proportion of kleptoparasitic gulls, i.e. great black-backed, male herring and Scandinavian herring gulls, increased and female herring gull feeding success declined.

The kleptoparasitic strategy itself may not be profitable under certain conditions. As the ratio of kleptoparasite to host increased one might expect a fall off in success as hosts become increasingly difficult to find. Whilst kleptoparasitism may continue to be a profitable strategy for the most dominant individuals, the more subordinate ones may switch to a different feeding method or give up altogether. There is evidence that this effect may operate for herring gulls when there is a high proportion of great black-backed gulls in the feeding flock. Under these conditions female herring gulls achieved a slightly higher swallowing rate than males in the first ten minutes from the start of feeding. There was evidence that many herring gulls opted to leave the feeding area after this time, presumably because they could no longer feed profitably, due to greater competition from great black-backed gulls. A similar mechanism has been proposed to explain differences in foraging behaviour in groups of feeding hyenas, Crocuta crocuta, (Tilson & Hamilton, 1984). In the areas where lions, Panthera leo, are present, hyenas consume carcasses rapidly and there is no evidence of a dominance hierarchy.

In contrast, where lions are absent, carcasses are consumed slowly, usually only one animal feeding at a time and there is a clearly developed dominance hierarchy with the dominant (and larger) female feeding first followed by her daughters, and the subordinate males last.

Although competitive ability in both herring and great black-backed gulls may be largely determined by body size, with experience also playing a part, quite subtle changes in flock composition, by altering the nature of competitive interactions, can have relatively large effects on comparative feeding success of the different species, race, sex and age groupings within the feeding flock.

6. GENERAL DISCUSSION

Although increased production of refuse over the course of this century has undoubtedly increased food availability all year round for gulls, this study has shown that there is a large amount of variation in the ability of individuals to exploit this food source successfully.

Some individuals tend not to feed at tips at all. A smaller proportion of immature herring gulls feed at refuse tips in northeast England than would be expected on the basis of the average age composition of the herring gull population (Monaghan, 1980). As a result of the highly competitive nature of feeding at a refuse tip and the skills required, many immature birds are unable to feed profitably there. Black-headed gulls use tips in varying numbers but are rapidly excluded by the larger gulls during competitive feeding. They can however, due to smaller body size, take advantage of disturbed feeding opportunities more profitably than the larger gulls. The extent to which black headed gulls participate in the more competitive undisturbed feeding is unfluenced by the number of large gulls present. Horton _et al_. (1983) recorded no competitive exclusion of black-headed gulls but, at all 20 tips in their study, numbers of black-headed gulls exceeded those of the larger gulls, the average ratio of small to large gulls being 5:1. There was also a significant negative correlation between the total number of gulls present and the ratio of small to large gulls (r_s=0.72, N=20, p < 0.01: calculated from data in Table 4, Horton et al., 1983). The situation at tips in northeast England is quite different, in that the average ratio of small to large gulls is approximately 0.4:1 and, under these circumstances, black-headed gulls are excluded from or avoid competitive feeding due to the high numbers of herring and great black-backed gulls present.

The working regime of the refuse tip also influences its relative attraction for different species. Burger (1981) has suggested that the increased practice of covering refuse with earth or sand, as soon as it has been dumped, results in more frequent bulldozer activity, and that this has favoured the exploitation of refuse by smaller gull species. This factor alone may have made refuse a less accessible food source for the larger gull species in recent years.

Sibly & McCleery (1983b) in a study of adult herring gulls during the breeding season found that, at refuse tips, females were less efficient foragers than males whereas there were no differences in feeding efficiency between the sexes at other feeding sites. The lower efficiency of females was attributed to their subordinate status in competitive interactions. This study has shown that the nature of the feeding opportunities at a refuse tip are such that, on average, 40% of undisturbed (i.e. competitive) feeding bouts last for less than ten minutes and over this time no difference in feeding performance between the sexes was demonstrated. It is only when feeding continues for longer that the competitive disadvantage of females becomes apparent, as the level of aggression increases due to the depletion of edible items from the refuse. Some females then respond by leaving the feeding area and this is reflected in the lower participation of females in undisturbed feeding compared to males (Chapter 3). Females also tend to feed more often in the edge areas of the refuse where food return is lower but aggressive interactions are less frequent (Monaghan, 1980). There was however no overall difference in the average time spent feeding each day between the sexes because females were able to compensate for reduced participation in competitive feeding by a corresponding increase in disturbed feeding (Chapter 3).

The influx of the larger Scandinavian herring gulls to refuse tips in the northeast, especially in December and January (Coulson _et al_., 1984a) might be expected to have a deleterious effect on the performance of their smaller British counterparts. However at the same time as the proportion of Scandinavian herring gulls at the tips increases, so does that of great black-backed gulls (Chapter 5). Aggression is correlated with body size (Chapter 4) and so this shift in flock composition towards larger individuals results in a corresponding increase in the frequency of aggressive interactions. In addition both herring and great black-backed gulls attack aggressive birds preferentially; i.e. aggression begets aggression (Chapter

5). Scandinavian herring gulls are larger and therefore more aggressive than British herring gulls and consequently they are attacked by great black-backed gulls with greater frequency than are British herring gulls. Therefore, although Scandinavian herring gulls are the victims of conspecific attacks less often than British herring gulls, the overall rate at which individuals of the two races are attacked is similar, as is the feeding success achieved. The number of Scandinavian herring gulls which travel further south and further inland during the winter (Stanley et al., 1981) may result from attempts to escape competition from great black-backed gulls which tend to remain near the coast.

In competitive feeding, behaviour is closely linked to body size, such that sex-related differences are also explicable in these terms (Chapter 4). The smaller birds (i.e. British female herring gulls) obtained most of their food by active, independent foraging. Larger birds, by increased aggression, exploited the searching efforts of others to locate and obtain food. The extent to which the latter strategy was employed by individual birds increased with increasing body size. These two foraging strategies are an example of a general model for interactions between and within species put forward by Barnard & Sibly (1981) involving 'scrounger' individuals or species which exploit a limited resource which is provided by 'producers'. Such a model describes a biological game where the fitness of scroungers is strongly frequency dependent, and in which stable coexistence is dependent on the fitness of scroungers being higher than that of producers when the former are rare, but lower when scroungers are common (Barnard & Sibly, 1981). Within this framework there are two possibilities; a) all individuals may be able to adopt either strategy, or b) the strategy of each individual may be limited by its phenotype. At the population level these two situations are indistinguishable, but if individuals can be recognised then phenotypic limitations can be identified. This study has shown that, at refuse tips, the phenotypic limitation of body size is sufficient to explain the use of different feeding strategies by individuals of different species and of different race and sex in the case of herring gulls. Situations where the choice between alternative strategies is determined by body size are common in nature. Parker (1984) gives several examples from studies of alternative mating strategies in insects where the strategy adopted is determined by body size (e.g. Thornhill, 1983). In vertebrates size often increases with age and then the strategy chosen by an individual may change when it reaches a certain age, i.e. there is a life history switch from one strategy to another (e.g. Clutton-Brock et al., 1979). In the herring gull foraging experience also acts as a phenotypic constraint on foraging strategy. Immature birds have a feeding strategy which depends heavily on other feeding birds for locating and obtaining food, but they gradually switch to a more independent strategy as they acquire feeding skills (Chapter 2).

In the natural feeding situation investigated in this study, flock composition was variable and this allowed frequency dependent effects to be investigated. However the variation was not continuous since seasonal effects and local weather conditions tended to act together to bring about a discrete change from predominantly small herring gulls (females) and a small number of great black-backed gulls to larger herring gulls (more males and more Scandinavians) and a high number of great black-backed gulls. The effect of this shift in flock composition was that when the proportion of kleptoparasitic individuals (i.e. scroungers) in the flock was small, the feeding success achieved by all members of the flock was similar. As the proportion of scroungers increased, their feeding success increased, whereas that of the producers (mainly female herring gulls) declined. Thus the frequency dependent effect on the producers was as expected but not so that on the scroungers. The change in the frequency of scroungers in the population may have been accompanied by a change in the 'quality' of individuals. The increased age of the herring gulls present when the frequency of scroungers was high (indicated by the change in average male bill depth) may have contributed to their increased success. Under these circumstances there was a shift in sex ratio of great black-backed gulls towards males, and since in the feeding behaviour data the sexes were not distinguished, this sex ratio change may have contributed to increased success. Great black-backed gulls selectively attack conspecifics and the proportion of attacks leading to food gain is higher in conspecific attacks than when they attack herring gulls (Chapter 5). Thus, as the frequency of great black-backed gulls increases, a greater proportion of their attacks are directed at conspecifics; such attacks are more successful, and hence their overall feeding rate increases. It is apparent that a mixed species feeding flock, such as that described in this study, is not simply a two-tier system of producers and scroungers but something more analagous to a food chain or food web with several different groups of scroungers, all varying in competitive ability.

Feeding at a refuse tip therefore involves many complex interactions and competitive skills and so it is not surprising that immature herring gulls take several years to learn to exploit this food resource fully. Over the first four years of life the foraging behaviour of herring gulls gradually changes:

a) they become less aggressive

b) they become more successful when attacking both in terms of displacement of the opponent and in terms of the proportion of attacks which lead directly to food gain

c) they learn to use aggression rather than swallowing in other feeding birds as a cue for making attacks

d) they make fewer attempts to steal food from adults

e) they obtain a greater proportion of food from independent foraging

f) food intake, as measured by swallowing rate, increases.

In these ways, herring gulls gradually become more skillful both at independent foraging (locating and extracting edible items from refuse) and in obtaining food through competitive interactions. Social learning is likely to be important in both cases. Copying behaviour of various kinds has been shown to increase success both in locating and in capturing food (Murton et al., 1971; Krebs et al., 1972; Rubenstein et al., 1977). Groves (1978) showed that juvenile ruddy turnstones are less adept at interpreting and responding to the signals of older birds and as a consequence they are involved in a greater number of aggressive encounters than adults. Social rank gradually improves with experience in aggressive encounters. Improvements in feeding success or efficiency with age have been demonstrated in a number of seabird species (see 2.1 for examples) and are likely to be characteristic of any species which is dependent on a 'difficult' food supply, i.e. one where skills need to be learnt before the resource can be fully exploited (e.g. Schaller, 1972; Arnold & Dudzinski, 1978). Delayed maturity in seabirds has been linked to the need for individuals to attain a certain threshold in feeding efficiency before they are able to take on the additional costs of breeding (Ashmole, 1963). The majority of herring gulls do not breed until the fourth or fifth year of life. This study has shown for at least the first four years (and in some cases longer - see below), they are gradually learning and improving those feeding skills necessary to feed successfully at a refuse tip. Thus, although the food available for gulls may have increased over this century, the reproductive output of the species is still limited by length of time necessary for the acquisition of feeding skills.

In this study use has been made of the fact that bill depth in herring gulls continues to grow after maturity, whereas other body measurements such as wing length or head and bill length do not (Coulson et al., 1981). A difference in average bill depth, in the absence one in head and bill length therefore is indicative of a difference in average age. On this basis a number of age-related trends in adult male herring gulls were demonstrated

a) the average age of male herring gulls feeding at tips declined seasonally (Chapter 3)

b) the average age of males in competitive feeding increased as the feeding bout progressed (Chapter 3)

c) feeding success in males increased with age (Chapter 4)

There were no size-related trends in females, which suggests that such effects may be related to dominance in competitive interactions. I suggest that bill depth itself acts as a signal of social rank (whether or nor directly associated with age) and this may explain why this measurement continues to increase in adult life and also why the rate of increase should be greater in males than in females (Coulson et al., 1981).

Refuse tips provide a variety of feeding opportunities and the feeding methods used by individuals of different species and of different age, sex and race, in the case of the herring gull, are not dissimilar from those required at other feeding sites. Gulls often feed in high density flocks at concentrated food sources where competitive interactions are frequent e.g. on fish shoals near the surface or scavenging at fish quays. At some feeding sites there is a high requirement for manoeuvrability, e.g. feeding behind the plough or surface dipping for scraps of raw sewage at a sewage outflow. Other feeding sites may require more active, independent foraging e.g. feeding for worms on pasture or for mussels on the shoreline. Thus, the constraints on foraging behaviour, namely age and experience, body size and the composition of the feeding flock are likely to be generally applicable to the feeding ecology of herring, great black-backed and black-headed gulls.

Whilst refuse tips are of considerable importance to wintering herring and great black-backed gulls in particular, the question of the role that this food source might play in determining winter survival, and even reproductive success in the following breeding season, requires further information on the relative feeding behaviour and performance of individuals at other feeding sites during this time. Tips may be less preferred feeding sites for some herring and great black-backed gulls in that both species feed there in increased numbers when the weather is severe and other foods are scarce (Chapter 4). Five or ten fold increases occur in great black-backed gull numbers whereas the change in herring gull numbers is usually proportionally less. The changes in flock composition indicate a degree of feeding separation between the sexes for both great black-backed and herring gulls, with more females of both species normally feeding inland at refuse tips and correspondingly more males using preferred feeding sites on the coast (Chapter 5). Ideally, an assessment of the relative merits of different feeding strategies requires some measurement of both the costs incurred and the benefits obtained. The relative nutritional value of different gull foods is hard to assess. Calorific values for refuse are extremely misleading as they are calculated from the total combustion of 'whole refuse' which, particularly in more recent years, contains a high proportion of plastics, which contribute heavily to the overall calorific value but which are of no nutritional value (Sumner, 1971). If gulls are selective in what they take, as is suggested by the need for young birds to learn what is edible and what is not, this presents further difficulties. Clearly comparisons of feeding success based simply on swallowing rates beg the question of what it is and how much of it that the bird is swallowing.

Calculations of the energetic costs of foraging based on theoretical values are subject to large errors and take no account of the individual variation which is clearly of importance. Ideally, behavioural observations and time budget analysis, such as has been presented here, should be combined with some measurement of the metabolic costs of different activities along the lines of the work of Bryant & Westerterp (1982).

This study has demonstrated that feeding at a refuse tip is a complex process. Individual birds are presented with a number of feeding opportunities which differ as to their duration and as to the nature of the feeding methods required. That different individuals do make different choices and that these choices are related to constraints such as body size, is evidence of a degree of assessment of the relative profitability of different strategies. Although the food supply is temporarily abundant, access to it is restricted and so a premium is placed on foraging efficiency. Herring gulls take at least four years to improve their performance in competitive interactions and to develop the skills necessary to exploit this food source successfully.

There is a considerable need for further work on the feeding performance of herring gulls and the nature of the inter- and intra-specific interactions which occur at other feeding sites, such as at sea.

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Appendix A

List of the environmental variables considered for the multiple regression analysis on the number of herring, great black-backed and black-headed gulls visiting refuse tips in northeast England throughout the winter. An asterisk denotes those variables which were subsequently used in the analysis (see Chapter 4).

Records from Tynemouth

*1. Air temperature at 0600h in degrees celcius

2. Air temperature at 1800h on the previous day in degrees celcius

*3. Wind speed at 0600h in knots (1 knot=1.85 km/h)

*4. Wind speed at 1800h on the previous day in knots

*5. Wind direction at 0600h coded follows:
0 - offshore; 1 - onshore

6. Wind direction at 1800h on previous day (coded as above)

*7. Size of the fish catch landed at North Shields from inshore and offshore vessels in cwt (1 cwt=50.8 g) and converted to natural logarithms

8. Size of the fish catch landed at North Shields on the previous day (measured as above).

Records from Durham Observatory (readings taken at 0900h unless otherwise stated)

9. Minimum temperature in degrees celcius

10. Maximum temperature in degrees celcius

*11. Frost coded as follows:

1 - no overnight frost; 2 - overnight frost

12. State of the ground coded as follows:

1 - ground dry, moist or wet; 2 - ground partially or totally covered with ice or snow

13 Rainfall

14 Wind speed in knots