Short communication

Differential daytime distribution by age in Black-headed Gulls *Larus ridibundus*: adult physical dominance or competitive superiority?

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The ideal free distribution model (Fretwell & Lucas 1970) and later developments (Sutherland 1996) have been successful in explaining the spatial distribution of individuals in relation to resources. However, most studies have tested the distribution of either equal or unequal competitors under the continuous input model using relatively simple experiments (for examples, see Sutherland 1996).

For various species of birds it has been shown that different categories of individual (sex, age) tend to be spatially segregated during foraging, and that this pattern is the result of one category being physically dominant over other categories, excluding them from preferred sites (Cresswell 1994, and references therein). Since travel costs from a roost site to a foraging area probably influence the profitability of the latter, feeding sites nearest to the roost may contain the competitively superior individuals.

During studies of the kleptoparasitic behaviour of Black-headed Gulls *Larus ridibundus*, we noted an apparent difference in the spatial distribution of adult and young individuals. This observation prompted us to collect data on adult:juvenile ratios in foraging flocks of gulls and to examine the ratios in relation to the distance from the night roosts. To try and understand the reasons for the differential distribution of age categories, we also studied differences in their foraging proficiency and behaviour at a reservoir in the city of Malmö.

METHODS

The study was conducted during the autumns of 1995 to 1998 in Skåne, southern Sweden. Some data on the age ratio in gull flocks were recorded opportunistically, but the majority was collected by driving predetermined routes, usually either starting inland going towards the coast, or starting from the coast going inland. Skåne has coast on three sides: the Sound to the west and the Baltic to the south and east; routes reached the coast on all sides from the northwest to the northeast. In addition, some routes were restricted to the inland of south central Skåne. All these areas are predominantly agricultural land. Disregarding built-up areas, in most parts where observations were made, arable land makes up more than 75% of the area, in some parts close to 90%, with winter wheat, sugar beet and oilseed rape being the dominant crops.

Data were collected during 20 September to 9 November in 1995, 4 August to 21 November in 1996, 30 August to 4 November in 1997 and 14 August to 24 October in 1998. During this autumn period, agricultural activities included harrowing, ploughing and mechanized extraction of sugar beets, all of which attract gulls, especially ploughing which seems to expose the largest number of earthworms, the gulls' main food. A few flocks of gulls kleptoparasitized Lapwings *Vanellus vanellus* and Golden Plovers *Pluvialis apricaria*. In each flock of Black-headed Gulls (or mixed gull flocks containing Black-headed Gulls), we counted the number of adults and juveniles (birds fledged in the current year; these are easily separated from older birds on plumage characteristics, Cramp & Simmons 1983). Sometimes not all gulls in a flock could be aged, e.g. because some were hidden behind other gulls or behind obstacles, or because total numbers were very high. However, in two-thirds of the flocks all individuals were aged, and in four-fifths more than 90%; in the remaining flocks (very large ones) samples most often consisted of more than half of the gulls in the flock. Flocks included in the following analysis numbered from 12 to about 1000 Black-headed Gulls.

Data collection was not standardized with respect to time of day. However, the pattern reported below was apparent all day from shortly after dawn until the gulls left for the night roosts in late afternoon.

In autumn, Black-headed Gulls in Skåne roost during the night at the coast and on two of the larger lakes, Lake Vombsjön and Lake Ringsjön, both about 33 km from the western coast and slightly farther from the eastern coast. The roosting sites of flocks were confirmed in several areas, but the exact roosting sites of most flocks were not known. Therefore, for each flock we measured the straight-line distance to the nearest coast or the nearest one of the two lakes, whichever was closest.

During the first three autumns we also investigated differences in foraging proficiency between adult and juvenile Black-headed Gulls by some simple trials. These were carried out at a large reservoir in central Malmö (Pildammsparken) and consisted of throwing small cubes of bread to the gulls in a standardized fashion and noting the numbers taken by adults and juveniles, respectively. The mean number of adults was 24.6 ± 16.4 sd and that of juveniles 13.7 ± 5.4 during these trials. The number of

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bread cubes taken by the gulls varied from 41 to 277 between trials, with a mean of 151.1 ± 66.6. Subsequently, we related these numbers to the weighted mean number of gulls of the two age-classes and calculated a ratio of juvenile to adult success rate for each trial. On nine days we also recorded the proportion of pieces captured in the air and on the water by the two age categories.

RESULTS

Spatial distribution of the age categories

In Figure 1 the proportions of juvenile gulls in the flocks are plotted against the distance to the nearest coast or roosting lake; the proportion of juveniles increases steeply with increasing distance ($r_{363} = 0.806$, two-tailed $P < 0.001$).

Although the number of flocks of Black-headed Gulls observed in any one day was small (up to 12), the pattern of increasing proportions of juveniles with increasing distance to the roost was consistent in all four years, for all routes, and from early August to November. The distribution of the age-classes was the same from the first morning hours until late afternoon and did not result from adult gulls leaving towards night roosts earlier than juveniles.

Thus, there was no bias caused by regional, seasonal or diurnal variation in the proportions of the two age categories. Neither could we find any differences with respect to the food sources or feeding methods used by the two age groups – with two exceptions: both at the reservoir in Malmö and during 'hawking' for insects near the coast the proportions of juveniles were higher than expected from the distance to the roost; data not included in Figure 1.

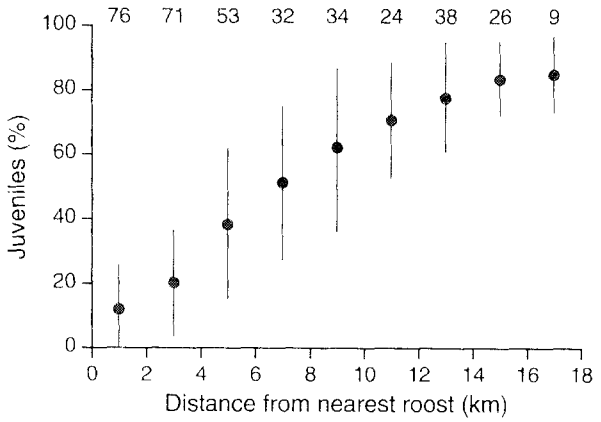

Figure 1. The percentage of juveniles in flocks of Black-headed Gulls at different distances from the known or presumed roosts (see Methods). Results are means (± sd). The number of flocks in each distance category is given above the sd bars.

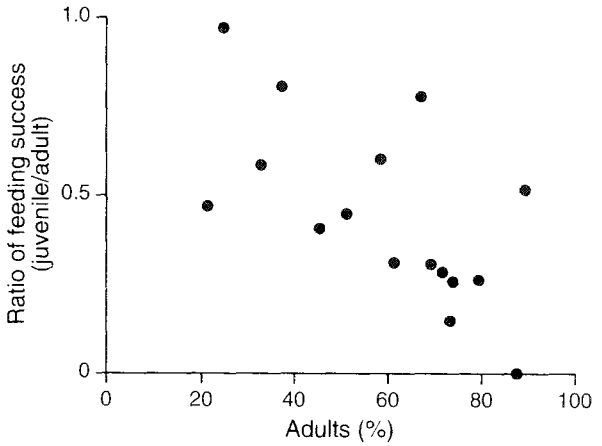

Figure 2. Juvenile feeding success in relation to percentage of adults in the flock during 16 trials at Pildammsparken, Malmö. Success is expressed as the ratio of the mean number of pieces of bread taken per juvenile to the mean number taken per adult. The regression line is $y = 0.895 - 0.008x$, $P = 0.008$.

Age-related foraging proficiency

The results of our trials at the reservoir in Malmö suggested an interesting effect. Using samples obtained from mid-October until mid-winter when both age categories of gulls seemed highly motivated to take bread, the ratio of juvenile success rate to that of adults decreased with increasing proportions of adults in the flock ($r_{s16} = -0.67$, two-tailed $P < 0.02$, Fig. 2). Thus, the higher the proportion of adults, the less successful was the average juvenile.

Our trials also demonstrated clearly that: (1) during the whole autumn (and winter), the adults were much more proficient than the juveniles at capturing the pieces of bread; (2) the adults caught most of their pieces in the air ($\bar{x} = 67.6 \pm 18.9\%$ vs only $17.3 \pm 11.2\%$ for the juveniles); (3) whereas the juveniles fought fiercely for pieces that had reached the water, except during the most severe winter situations, the adults avoided fights and normally just quickly snatched such pieces from the surface.

Observations of mixed-age gull flocks feeding behind the plough are consistent with our results from Pildammsparken. During 13 counts on five days of the 6–19 gulls on the wing closest to the plough (as it passed a predetermined reference point), the proportion of adults always was around 80%, whereas among the 11–35 birds that stayed behind in the furrows near the plough's turning point searching for food on foot, the proportions were reversed, with on average less than 20% adults (these differences were statistically significant; Fisher exact test, $P < 0.001$ in all cases). Thus, also at a small scale, there was a certain degree of spatial segregation, apparently related to differences in foraging proficiency between the age-classes, with the adults closest behind the plough where most earthworms become exposed.

Interestingly, on 12 September 1998 when Black-headed Gulls were hawking for swarming insects (most

likely ants) in thermals close to the seashore and interference probably did not influence foraging success, the adult:juvenile ratio was close to unity. Among 168 gulls simultaneously feeding by 'dipping' in shallow water, the proportion of juveniles was less than 7%. However, it cannot be determined whether the predominance of adults in the latter situation resulted from a reduction in the juveniles' expected prey capture rate due to the presence of adults or whether juveniles simply had a higher net energy gain from hawking insects than from dipping, regardless of any effect of presence of adults.

DISCUSSION

No doubt agricultural activities, notably ploughing and harrowing, provide the gulls' most important source of food during autumn in Skåne, and on some days practically no gulls are seen feeding in other situations. Such activities, therefore, play an important role in determining the distribution of gulls in the agricultural landscape.

Reasons for differential distribution of the age-classes

Adults made up about 80% or more in flocks within the 4 km zone closest to the known or presumed night roosts, whereas they constituted less than 20% further than 14 km from them. Also among Black-headed Gulls and Common Gulls *Larus canus* wintering in Belgium and the Netherlands, there was a similar trend with higher percentages of juveniles inland than near the coastal roosts (Vande Weghe 1971). What is the mechanism behind this pattern?

As adults and juveniles use the same night roosts from which most of them fly inland to feed during the day, the most likely explanation is that some sort of competition exists between the two age groups, with the adults competitively superior to the juveniles, enabling them to choose feeding sites closer to the roost and thus avoiding time- and energy-consuming flights. If this is the case, what form does this competition take? Are the juveniles prevented from feeding, or is their feeding success lowered, by aggression from the adults?

Although Vande Weghe (1971) concluded that adults generally dominate juveniles (see also Ulfstrand 1979), this is questionable. In 82 out of 92 (89.1%) overt aggressive acts (threats and attacks causing the opponent to withdraw) recorded in autumn during studies of Black-headed Gull–Lapwing parasitism, the juvenile bird was the successful aggressor (H.K. unpubl. data, Andersson & Åhlund 1991, Smith & Metcalfe 1997). Also, during our trials at Pildammsparken, juveniles fought fiercely for pieces that had reached the water, whereas adults normally avoided getting involved in fights. Whether these observations can be extrapolated to the situation behind farm machinery, the dominant feeding site during autumn (pers. obs.), is so far unknown, but they nonetheless suggest that overt aggression may not be the cause of the observed distribution pattern of the two age categories.

Is there any other reason why it should be less profitable for juveniles to forage in the presence of adults? The results of our simple trials at Pildammsparken suggest that this may indeed be the case. There was a statistically significant tendency for the success of juveniles to decrease with the proportion of adults in the flock. This was not a result of aggressive interactions but of the adults' better skill at capturing the pieces of bread. The adults either circled in the air waiting for the pieces to be thrown or, when waiting on the water, were much faster than the juveniles in initiating flight once the piece was thrown. Vande Weghe (1971) made similar observations. When Black-headed Gulls were fed from building windows, the adults circled and captured the food in the air, whereas the juveniles waited on the ground below.

Monaghan (1980) and Monaghan *et al.* (1986), who studied the use of a rubbish dump by Herring Gulls *Larus argentatus*, found that the proportion of first winter birds decreased with an increased total number of birds at the most profitable site on the dump. Although feeding success was not measured, these results were interpreted as showing that juvenile Herring Gulls avoided competing with adults either because of dominance relationships or because the latter were much better at exploiting the food (see Greig *et al.* 1983 for a demonstration of the latter). A significant negative relationship was also found between the proportion of juveniles and the total number of Black-headed Gulls in a city park at Haren, The Netherlands (Hulscher 1985) and between immatures and flock size in Rooks *Corvus frugilegus* (Henderson & Hart 1991). In the latter study, immatures foraged less efficiently in larger flocks, apparently because avoidance of other individuals restricted their feeding.

Causes of variation in adult:juvenile proportions

Although the main pattern depicted in Figure 1 is very clear, there is also a considerable variance. There are several possible explanations for this and we briefly discuss three: (1) the proportion of juveniles in the population may vary seasonally; (2) the amount of agricultural activity may vary between days or periods; and (3) the total number of gulls may vary. The second two factors should influence the degree of competition.

The Black-headed Gulls in Skåne during autumn are mostly, or exclusively, birds on migration stopping over for unknown periods (Bengtsson 1996). As the proportion of juveniles recorded on migration at Falsterbo tends to vary between autumn periods (Olsen 1993), it is also likely to do so among those stopping over. The extent of this variation is, however, unknown.

On days when agricultural activity is low (few farmers ploughing), especially in the near-coastal zone, one would predict that adult gulls would fly further inland and that

the proportion of adults at a certain distance from the roost would be higher than on days when farming activity is high. There is some support for this in the data. For instance, on 3 October 1998, very little ploughing was taking place within 7 km of the south coast; none of five flocks found in that zone had more than 13% juveniles and higher proportions of juveniles were not found until more than 11 km inland. By contrast, on a couple of occasions a high proportion of juveniles was found close to the coast. Once three ploughs were simultaneously active in a huge field, on another a pasture that had remained under grass for many years was ploughed up, probably exposing more earthworms than normal to the gulls. On both occasions, the proportion of juveniles was much higher than expected from the relationship in Figure 1.

Also the total number of gulls, or rather the number relative to the sources of food, may influence the gulls' distribution. For instance, in late November 1997, when most gulls had migrated and we had ceased collecting data on flock composition, the proportion of juveniles was much higher than usual in some fields about 5 km from the coast. Likewise, in an area 10–14 km from the coast, where flocks were numerous during much of the autumn of 1998, no flocks were seen in late October despite intense farming activity there.

In summary, it seems that the pattern of increasing proportions of juvenile Black-headed Gulls the further one goes from the common roost site is somehow caused by the competitive advantage that age confers. This advantage appears to result from the adults' higher feeding proficiency that reduces the foraging success of juveniles. This in turn makes it advantageous for juveniles to fly to foraging sites further from the roosts. Clearly, detailed observations of behavioural interactions between age categories and measurements of feeding rates behind farm machinery are called for, but the data do suggest that travelling costs are important in ideal free distribution models. It would be interesting to know if the distribution pattern of the two age categories is still present in winter, for example in Britain with its large numbers of wintering Black-headed Gulls.

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REFERENCES

Andersson, M. & Åhlund, M. 1991. Hunger affects dominance among strangers in house sparrow. *Anim. Behav.* **41**: 895–897.

Bengtsson, K. 1996. Migratory routes and wintering areas of Swedish Black-headed Gull *Larus ridibundus* populations. *Ornis Svecica* **6**: 17–38. (in Swedish with English summary)

Cramp, S. & Simmons, K.E.L. (eds) 1983. *Handbook of Palearctic Birds*, Vol. 3. Oxford: Oxford University Press.

Cresswell, W. 1994. Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *J. Anim. Ecol.* **63**: 589–600.

Fretwell, S.D. & Lucas, H.L. Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* **19**: 16–36.

Greig, S.A., Coulson, J.C. & Monaghan, P. 1983. Age-related differences in foraging success in the herring gull (*Larus argentatus*). *Anim. Behav.* **31**: 1237–1243.

Henderson, I.G. & Hart, P.J.B. 1991. Age-specific differences in the winter foraging strategies of rooks *Corvus frugilegus*. *Oecologia (Berl.)* **85**: 492–497.

Hulscher, J.B. 1985. Habitat choice of juvenile and adult Black-headed Gulls *Larus ridibundus*: a choice between wet and dry. *Limosa* **58**: 49–56. (in Dutch with English summary)

Monaghan, P. 1980. Dominance and dispersal between feeding sites in the Herring Gull (*Larus argentatus*). *Anim. Behav.* **28**: 521–527.

Monaghan, P., Metcalfe, N.B. & Hansell, M.H. 1986. The influence of food availability and competition on the use of a feeding site by Herring Gulls *Larus argentatus*. *Bird Study* **33**: 87–90.

Olsen, K.M. 1993. The migration of gulls and terns at Falsterbo in the summer and autumn of 1991 and 1992. *Anser* **32**: 253–262. (in Swedish with English summary)

Smith, R.D. & Metcalfe, N.B. 1997. Why does dominance decline with age in wintering snow buntings? *Anim. Behav.* **53**: 313–322.

Sutherland, W.J. 1996. *From Individual Behaviour to Population Ecology*. Oxford: Oxford University Press.

Ulfstrand, S. 1979. Age and plumage associated differences of behaviour among blackheaded gulls *Larus ridibundus*: foraging success, conflict victoriousness and reaction to disturbance. *Oikos* **33**: 160–166.

Vande Weghe, J.P. 1971. Relations entre adultes et juveniles chez la Mouette Rieuse, *Larus ridibundus*, et le Goeland Cendre, *Larus canus*, en hivernage. *Gerfaut* **61**: 111–124.

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