FLOCK SIZE AND FEEDING EFFICIENCY IN HOUSE SPARROWS

There are several possible advantages which could be gained by individuals that choose to forage in groups rather than alone (Bertram 1978; Murton 1971). The principal currently debated benefits to birds that join flocks are those related to either increased probabilities of predator detection and avoidance (e.g. Caraco 1979; Lazarus 1979) or increased foraging efficiency (Krebs 1980; Rubenstein *et al.* 1977). Both types of advantage may be gained simultaneously in many cases. The purpose of this study was to further investigate one mechanism whereby individual foraging efficiency could be increased as a result of flock formation.

Several studies have suggested that a bird searching for patchily distributed and unpredictable food resources would be more likely to locate these resources if it joins a flock (see Bertram 1978 for a review). For example, birds flying in search of food patches should do better if they land near other birds seen feeding. Furthermore, individual birds within a foraging flock may learn about the location and nature of potential food sources by observing the feeding behaviour of other individuals (Murton 1971).

The experiments of Krebs *et al.* (1972) tested this idea, and showed that Great Tits *Parus major* placed in an aviary in groups were more likely to find a hidden source of food than were individuals tested alone. Their experiments used four birds as the only group size, and mealworms as the food (Great Tits are predominantly insectivorous). However, many small passerine birds are found in larger groups, and flocking behaviour is common among granivores as well as insectivores. We therefore devised a set of aviary experiments essentially similar to those of Krebs *et al.* (1972), but we used a granivorous species, the House Sparrow *Passer domesticus* with hidden grain as the food source, and we incorporated larger flock sizes in order to test the generality of their original experimental results. We have also examined the relationship between flock size and predator detection in this species (Elgar & Catterall 1981).

In the food-finding experiments, the transfer of information among flock members can be viewed as a type of social facilitation, in which the frequency of a particular behavioural pattern increases in individuals that are in sight of others performing the behaviour (Clayton 1978). The data collected in our experiments were, therefore, further analyzed in order to test for the occurrence of social facilitation in the experimental sparrow flocks.

EXPERIMENTAL METHODS

The experiments were conducted over a period of four weeks during the winter of 1979, with seven male and eight female House Sparrows caught in late autumn as immatures, colour-banded, and maintained for five months before the experiments. For several weeks the Sparrows were trained to forage within small feeding bowls (4cm diameter) which contained grain concealed by chopped newspaper. The numbers and positions of bowls with and without grain (but all filled with paper) varied from day to day, both before and during the experimental period, so that the birds did not form any expectations concerning the location of food. The feeding bowls were arranged on the floor of the aviary on a rectangular (140 by 160 cm), six by six grid.

Twenty-three experiments were conducted in order to test whether Sparrows placed in groups of four or eight birds were more likely to find a single patch of concealed grain than were solitary Sparrows. First, the experimental birds were released into the isolated experimental section of the aviary and allowed to settle down. Thirty-six food bowls, one containing half a teaspoon of grain and all filled with chopped newspaper were then placed on the grid points. Observations were made for twenty minutes after the first bird entered the foraging area (defined by the grid points) if no bird found food, or for five minutes after the first bird found food. The birds were observed through a one-way mirror, and the results were spoken by the observer and recorded onto a continuously running cassette recorder. Every visit made by an individual to a food bowl was recorded, and all successful feeders (birds that obtained food directly from the bowl) were identified. The experiments took place in the early morning or late afternoon, when House Sparrows usually feed in the field. All food was removed from the aviary the night before the morning experiment, and about two hours before the afternoon experiment. We conducted sixteen experiments using solitary birds (one randomly chosen bird was used in two experiments), then four experiments using flocks of four (randomly sorted), and then three experiments using flocks of eight (randomly sorted).

RESULTS

The proportions of solitary birds, birds in groups of four and birds in groups of eight that obtained food were 0.125, 0.875 and 0.792 respectively. A Chi-square Contingency Test for independence (2 x 2; df = 1) revealed that birds in flocks of four (χ^2 = 18.6) and flocks of eight (χ^2 = 17.1) had a significantly greater chance of obtaining food than solitary birds ($p < 0.005$), but there was no significant difference between flocks of four and eight (χ^2 = 0.46). All but two of the solitary birds actively searched for food during the experiment, so their poorer feeding success was probably not due to stress resulting from isolation. Aggressive interactions occurred in all 'flock' experiments, and consequently the amount of food eaten varied from bird to bird and some birds were prevented from feeding. In five of the seven experiments involving flocks, the individual that first found food was rapidly supplanted by another bird; one of these supplanting individuals had not attempted to forage for itself.

If the increased foraging success of Sparrows in the flocks was due to social facilitation, then those individuals that saw a neighbouring bird obtaining food from a bowl should have tended to increase their visit rates to adjacent bowls. This hypothesis was tested by calculating the frequency distribution of the number of times each bowl was visited during each experiment. The variance/mean ratio of the visits per bowl was then calculated for each experiment (Table I). The value of this ratio indicates (Southwood 1978) whether the frequency distribution is clumped ($S^2/\bar{X} > 1$), random ($S^2/\bar{X} = 1$) or evenly distributed ($S^2/\bar{X} < 1$). The variance/mean ratios in Table I were significantly greater ($p = 0.001$; Mann-Whitney U-test, $U = 1$; $n_1 = n_2 = 7$) after the first bird found the food, which indicates that subsequent investigatory visits to food bowls were more clumped. In other words, after the first bird found food, the other flock members rapidly moved to the food bowl and foraged in it and adjacent bowls. The mean number of times a bowl was visited by individuals was generally smaller after the food was found (Table I) because most of the bowls were not visited.

TABLE 1

Mean ($\bar{X}$), variance (S^2) and ratio of variance to mean of the number of times each bowl was visited before and after the first bird found food.

	Before			After		
	$\bar{X}$	S^2	$S^2/\bar{X}$	$\bar{X}$	S^2	$S^2/\bar{X}$
4 flocks of 4	1.19	1.27	1.07	0.81	1.17	1.44
	3.06	2.83	0.92	0.92	1.52	1.65
	1.03	0.97	0.94	0.61	1.02	1.67
	1.39	0.90	0.65	0.56	1.80	3.21
3 flocks of 8	2.69	2.04	0.76	1.25	3.91	3.13
	1.97	2.91	1.50	1.00	2.10	2.10
	0.47	0.36	0.77	1.03	1.64	2.60

DISCUSSION

The experiment showed that the Sparrows were more likely to find food when in flocks of four or eight than when searching alone. These results are consistent with those described by Krebs *et al.* (1972) for Great Tits and Rubenstein *et al.* (1977) for mixed species of seed-eating finches and suggest that this kind of feeding advantage to flocking birds may be successfully generalized across species.

The proposed mechanism of feeding advantage is socially facilitated behaviour, which occurs when the frequency at which an individual performs an activity increases when the individual can see others that are engaged in the same behaviour (Clayton 1978). Earlier experimental studies of House Sparrows have demonstrated socially facilitated behaviour (Porter 1904, 1906; Turner 1964; Watson 1970; Gallup & Capper 1970). However, these studies did not show that Sparrows consequently benefit from foraging in flocks through a feeding advantage. In our study this response resulted in the Sparrows clustering around the food bowl, with several birds frequently attempting to feed simultaneously. Aggressive interactions then occurred, which caused the exclusion of some individuals from the food bowl. The frequency of fighting was greatest in the flocks of eight; the proportion of birds that obtained food (.792) being slightly less than that for flocks of four (.875). Dominance relationships may have been intensified in the aviary, due to the non-renewable and spatially clumped food source. This may have decreased the success of some individuals in the flocks, but would not have affected the solitary birds; hence the results of our experiments would be conservative.

Baker (1978; but see Krebs 1980) re-analysed the data of Krebs *et al.* (1972) and suggested that, in the field, birds of low social rank should leave flocks since they are frequently prevented from feeding by dominant birds which may 'parasitize' their food-finding abilities. In this study one individual that fed successfully alone was subsequently unable to feed in two out of three experiments with flocks. However, in the field, subordinate House Sparrows may be less frequently excluded because the food is generally more dispersed (Barnard 1980a, 1980b; Krebs 1980). Finally, subordinate birds should still join flocks if the disadvantages of their low social status are outweighed by other advantages, such as those related to vigilance against predators (Barnard 1980a; Elgar & Catterall 1981).

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LEARNING BEHAVIOUR AT THE NEST OF THE COOPERATIVELY BREEDING YELLOW-RUMPED THORNBILL *ACANTHIZA CHRYSORRHOA.*

These observations were made in the Middlesex district of Manjimup in S.W. Australia. The behaviour of Yellow-rumped Thornbills *Acanthiza chrysorrhoa* nesting in an olive tree 2m from the back verandah and overlooked by the kitchen window, has been watched for four seasons. The birds are resident and seen all the year in an area of approximately 10 ha.

Yellow-rumped Thornbills are recorded as co-operative breeders (Immelmann 1960; Ford 1963), progeny of earlier broods assisting at subsequent nests. In nine nests between September 1977 and January 1980 the juveniles from the first brood were fed and tolerated in the nesting area while the female incubated a second clutch, but on hatching were chased from the garden. Whether the juveniles assisted with feeding their siblings after fledging was not known but none was seen at the nest.

On 29 May 1980 a pair, male orange/yellow (O/Y) and female white/red (W/R) began to build, they were a known pair who had been sexed by incubation patch and cloacal examination. On 12 June a third bird was seen carrying material to the nest and was identified as violet/violet (V/V). It was one of two young that fledged on 21 January 1980, from a nest in the olive of O/Y and W/R, the pair now building. At first materials brought by this helper were small and pushed at random into the general fabric, but as building proceeded more profiency was acquired in bringing better materials and more often. All the help was given to the male while the female worked alone in the brood chamber. At the end of June V/V was seen weaving material round vertical twigs. On 21 July the female began incubating three eggs in the brood chamber while O/Y and V/V continued adding to the false nest at the top of the already bulky structure above her. The resulting very large false nest at hatching time was almost enclosed at the top. The constructional methods were exactly the same as those used at the commencement of nest building i.e. an open cup nest gradually enclosed to make a circular brood chamber with a small entance hole. Identified materials used were dried grasses, spider's web, and bark from the vine. Feathers from domestic geese lined the brood chamber.

When the young hatched O/Y brought food for them and V/V flew to and fro with him, but carried nothing, and next day was not seen to take any part, but on the third day after hatching V/V, carrying a very small item, hopped onto a branch slightly below the brood chamber and poked it forward. Being so low the food went into the fabric, a second try had no greater success, and in a third attempt the prey was lost. In another twenty-four hours V/V was perching sideways to the nest entrance, thus a turn of the head was necessary to deliver the food and only if the female was brooding was it taken in