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PREY SELECTION AND SOCIAL BEHAVIOUR IN WAGTAILS (AVES: MOTACILLIDAE)

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INTRODUCTION

All predators are confronted with a series of problems when hunting for their prey: Solitary or flock foraging? Where to feed? Which prey to select? Which feeding technique to use? When to leave for another food patch? As Orians (1971) has pointed out, we would expect natural selection to favour those individuals which solved these problems in the most efficient way for two main reasons. First, there is some evidence that food is short in nature (Lack 1954, 1966). For example, in winter both titmice (Paridae) (Gibb 1960) and wagtails (Motacillidae) (Davies 1976) spend over 90% of the day feeding and procure one insect every few seconds. Under such conditions there must be a high premium on efficient foraging behaviour. Secondly, even if food is not in short supply, efficient foraging would still be favoured because this would enable the animal to spend more time in other activities.

Many recent studies have examined feeding behaviour in terms of optimization. One of the problems in such studies is choosing a currency and most models have used maximization of food intake per unit effort as a measure of feeding efficiency (Royama 1970; Schoener 1971; Krebs 1973; Krebs, Ryan & Charnov 1974).

In this paper I examine the ways in which wagtails solve these problems and discuss to what extent their feeding behaviour can be considered as optimal by the criterion of energy intake. I have studied two species, the pied wagtail (*Motacilla alba yarrellii* Gould) and the yellow wagtail (*M. flava flavissima* Blyth), both of which are small insectivorous birds inhabiting open country; they feed by picking prey up from the surface or by catching it in mid-air during a short sally from the ground.

Wagtails are a good subject for field work on feeding behaviour for several reasons. First, they are easy to observe and sometimes it has proved possible to keep a continuous watch on particular individuals throughout the day (Davies 1976). Secondly, in the relatively simple two-dimensional habitat of meadowland where the wagtails feed, it is possible to obtain simple measures of the food present. Thirdly, I have used a method for determining prey eaten based on an analysis of remains in faeces and wagtail faeces are easy to find. Finally, foraging wagtails occur both as singles and in flocks (Zahavi 1971; Davies 1976) so it is possible to compare the feeding behaviour in these two different social situations.

METHODS

Study area

All the observations were made on Port Meadow, an area of open grassland 3.2×0.8 km near Oxford. The grass on the meadow was grazed short by cows and horses which

were present all the year round. Parts of the meadow were flooded during the winter and these floods usually remained until early May.

Feeding behaviour

Pied wagtails were present on the meadow throughout the year, but yellow wagtails, which are summer visitors to Britain, were only present from early April until September. Most of the observations were made from March to May in 1974 and 1975, when both species were present. At this time the birds had not yet started to breed and observations were on adults which visited the meadow primarily in order to feed. From twenty to 100 pied wagtails and ten to sixty yellow wagtails were present each day during this period. None of the birds were colour ringed which meant that I could not recognize individual birds. The observations probably refer to well over fifty individuals of each species.

Two situations were studied in detail, namely the feeding behaviour of wagtails which were feeding on insects round dung pats and the behaviour of birds feeding on insects resting on the water surface in a shallow, flooded part of the meadow. Foraging birds



FIG. 1. Feeding experiment with a captive pied wagtail. Relationship between prey eaten and wing remains in faeces. Percentage of diet that consisted of Scatophagidae compared with the percentage of wings in faeces which were of Scatophagidae, the remainder of the prey being Sphaeroceridae.

were watched through binoculars at a distance of 20–30 m. Observation periods lasted from 1–10 min and the following events were spoken continuously into a tape recorder as they occurred; species of wagtail, single or flock, prey capture attempts, feeding technique and size of prey caught. The tapes were later played back together with a running stop watch to determine the time of each event.

Prey taken by the wagtails

I have used analysis of remains in droppings to determine prey taken by the wagtails. This method has been criticized by Hartley (1948) on the grounds that some prey remains will be over-represented in the faeces because of differential digestion. However, I have shown that, at least for wagtails, where most of the prey remains are of insects which with practice are easily recognizable, there is a good agreement between estimation of food taken using an emetic and the analysis of remains in droppings (Davies 1976). During this

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study almost all the prey were flies (Diptera). To test the validity of the dropping analysis method further, I fed a captive pied wagtail with different proportions of two flies which wild wagtails often encountered on the meadow. One of these were flies of the family Sphaeroceridae, 3–4 mm in length, while the others were flies of the family Scatophagidae, 5–10 mm in length. Droppings were collected from the captive bird at 30-min intervals after each feeding trial and then examined under a binocular microscope. Remains found in the droppings included heads, parts of the exoskeleton, legs and wings. Wings were the most convenient remains to quantify because most of them were whole and in good condition and because different families of flies have different wing venation and thus are easily recognizable (Plate 1).

Figure 1 shows that there was an excellent agreement between the proportion of the two flies given to the wagtail to eat, and the proportion of wings of the two flies which were recovered in the droppings. There was no difference in the recovery of wings for the

 Table 1. Feeding experiment with a captive pied wagtail, comparing the number of wings of prey recovered in droppings with the number given to the bird to eat

Prey		Total nul	liber of wings	°/ recovered
		Given in diet	Recovered in faeces	
Scatophagidae	5–7 mm	63	15*	
	8–10 mm	93	22*	
	Total	452	152	33.6
Sphaeroceridae	3–4 mm	192	58	30.2

* In addition several broken fragments were recovered which could not be measured. The number of wings that these represented were estimated for the total column by counting fragments which included the posterior cross vein.

 Table 2. Feeding experiment with a captive pied wagtail, showing the time after ingestion that wing remains of prey appeared in the faeces

Time (min) after ingestion

% wings recovered	30	60	90	120	180
Scatophagidae	26.3	57.9	86.8	97.3	99.9
Sphaeroceridae	9.1	50.0	77.3	95.5	99.9
Total	20.0	55.0	83.3	96.6	99.9

Cumulativa

two prey types, about a third of those ingested being found in the droppings (Table 1, $\chi^2 = 0.231$, 1 df). This was almost certainly an underestimate because some of the droppings on the cage floor were probably overlooked. In feeding trials with young spotted flycatchers (*Muscicapa striata* (Pall.)), I have recovered practically all the wings of prey given to the birds (in preparation). The results show that the small wings of the Sphaeroceridae are not more likely to get lost in the droppings than the larger wings of Scatophagidae, and this also holds for different sizes of wing within the Scatophagidae themselves (Table 1, $\chi^2 = 0.028$, 1 df).

There was no difference between the two prey in the rate at which they passed through the gut (Table 2). The first wings were voided 15 min after ingestion and although wings continued to appear in droppings produced 3 h later, over 80% had appeared by 90 min after ingestion. The wagtails usually spent the whole day on the meadow and often fed for several hours at a stretch in each of the two feeding areas that I studied them, namely the flooded pools and dung pats. Therefore the time the birds remained in the study area was long compared with the rate at which food passed through the gut, so that most of the droppings contained remains of food actually collected in that area rather than elsewhere.

The conclusion from this experiment is that, at least for flies, the analysis of wings in droppings gives a good indication of the proportion of prey eaten by wagtails. Droppings were collected from wild birds, mainly by searching the sites where individuals had been resting, and were stored in 70% alcohol and then later analysed in the laboratory. Most of the wings were in good condition, many of them whole, and therefore an indication of the size of prey taken could be obtained by measuring the length of wings in the faeces, which is related to body length. The results of this study are based on an analysis of over 10 700 wings found in the droppings of wild wagtails. Bryant (1973) has also used this method in a study of prey selection by the house martin (*Delichon urbica* (L.)).

Prey available

When wagtails were feeding on flies caught on dung pats, the number and species of prey available was assessed by direct counting of the prey on 100 dung pats, during a straight line transect across the meadow. Each pat was approached very cautiously to avoid disturbing the prey from the dung. When the wagtails were feeding in a shallow flooded part of the meadow, by picking up prey from the water surface, the available prey was sampled using a series of ten water traps, consisting of dishes of water with a little detergent added (Southwood 1966). Flying prey which landed on the water surface sank to the bottom and were caught.

RESULTS

The feeding behaviour of wagtails in flocks

Three situations were studied in which wagtails fed in flocks. A flock of ten to sixty pied wagtails fed over a flooded part of the meadow in March 1975, and a flock of fifteen to twenty-five yellow wagtails did so in May 1974. The water in the flooded areas was shallow, so that the birds could walk across the pools and pick up prey resting on the water surface. In 1975 the pools had dried up by April, when the first yellow wagtails arrived, but a flock of ten to thirty fed in the grass in the centre of the meadow.

Analysis of droppings of these flock birds showed that they fed almost entirely on Chironomidae, though the yellow wagtails in May 1974 also took large numbers of Drosophilidae (Table 3). There were vast numbers of Chironomidae on the meadow in the spring and the flock birds obviously took advantage of this abundant food supply and fed at a very fast rate (Table 4). Often a bird picked up twenty chironomids from the same spot without moving at all, and foraging individuals often recrossed their own paths or followed in the footsteps of others without any drop in their feeding rate. Although the diet of the yellow wagtail flock in April 1975 was very similar to that of the pied wagtail flock in March 1975, the feeding rate was only half as great, which may have been due to a decrease in the number of midges available.

Birds in the flocks showed very little aggression towards each other and often fed less than 1 m from neighbours. In a 3.5 h watch only three brief chases were observed in a flock of thirty yellow wagtails. The flocks behaved as single units, all individuals moving in the same direction at once, and when disturbed the whole flock flew off together to a new feeding area.

Wagtails fed in three main ways. They walked and picked up prey items from the ground

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surface (picking), they made a quick darting run at a prey item and picked it up either from the ground or as it took off (run-picking) and they made a short sally up off the ground and caught prey in mid-air (fly-catching). In all the flocks, individuals used the picking technique almost exclusively (Table 4).

The feeding strategy of the yellow wagtail flock in the flooded pools in 1974 was studied in more detail by comparing the prey eaten, as measured by wing remains in droppings, with that available on the water surface, as sampled by the water traps. Table 5 shows

		%	remains in droppi	gs Yellow Wagtail April 1975		
Prey	Body length mm	Pied Wagtail March 1975	Yellow Wagtail May 1974	Yellow Wagtail April 1975		
Chironomidae	2-3	96.7	34.8	85.9		
Drosophilidae	2-3	0.1	44.1	0.0		
Scatophagidae	5-10	0.6	2.0	4.8		
Sphaeroceridae	1-2	0.1	0.8	0.1		
Sphaeroceridae	3-4	0.1	4.6	3.4		
Sepsidae	3-4	0.0	0.1	0.0		
Chloropidae	2-3	0.1	0.0	1.4		
Ichneumonidae	2-3	0.0	3.4	0.0		
Aphididae	2-3	0.0	4.3	0.0		
Coleoptera	2-3	1.2	1.4	1.2		
Others*		1.1	4.5	3.2		
Total remains		4654	2862	1335		
No. days samples		9	10	5		

Table 3. The prey eaten by flock wagtails

* Includes the following prey: Calliphoridae, Mycetophilidae, Lonchopteridae, Syrphidae, Bibionidae, Tipulidae, Agromyzidae, Opomyzidae, Dryomyzidae, Empididae, Asteiidae, Tephritidae, Symphyta, Delphacidae, Neuroptera, Araneae.

Tab	le 4.	. Feeding	techniques	and fee	eding rai	tes of	flock	c wagtails

	Pied Wagtail March 1975	Yellow Wagtail May 1974	Yellow Ŵagtail April 1975
Feeding techniques			
% picking	100·0	99.9	99.6
% run-picking	0.0	0.0	0.1
% fly-catching Total capture	0.0	0.1	0.3
attempts observed	3200	3400	2440
Feeding rate			
items per min mean ± 1 S.E.	$73 \cdot 2 \pm 3 \cdot 3$	29.1 ± 1.5	$35\cdot 8\pm 1\cdot 2$
(n = no. of observation periods)	(23)	(142)	(63)

that although three prey types were common on the pool surface, the wagtails only took large numbers of Chironomidae and Drosophilidae and took very few Ichneumonidae. Inspection of the pool showed that there were vast numbers of Ichneumonidae resting on blades of grass emerging from the water, whereas most of the Drosophilidae and Chironomidae were resting on the water surface itself, flying off when disturbed and landing again a little further on. To have exploited the Ichneumonidae most effectively the wagtails would have had to move slowly amongst the vegetation searching in the leaves and this may have resulted in a reduced pecking rate. They did not do this, but remained in the open water picking up prey on the water surface. All the prey were of the same size, about 2-3 mm in length. It is possible that the wagtails were using prev activity as a searching cue and thus taking the active prey, namely the two families of Diptera, and ignoring the sluggish Ichneumonidae. However, in other situations wagtails do eat large numbers of Ichneumonidae.

The prey available and prey taken were compared for ten consecutive days while the flock were feeding in the pool. The numbers of Chironomidae and Drosophilidae caught in the water traps varied greatly from day to day. On some days the Chironomidae were the most abundant prey available while on others the Drosophilidae were the most

Table 5. Prey selection by a flock of yellow wagtails, May 1974, feeding on a flooded pool; comparison between prey available, measured by prey caught in water traps, and prey eaten, measured by remains in droppings ~ /

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Prey	sample	droppings
Ichneumonidae	30.1	3.4
Chironomidae	43.8	34.8
Drosophilidae	17.6	44.1
Others	8.5	17.7
Total	4328	2862
No. days samples	10	10



FIG. 2. Relationship between the number of Drosophilidae in the traps and the percentage of diet which consisted of Drosophilidae, in the yellow wagtail flock, for ten days, $r_s =$ 0.176, P > 0.05.

numerous. The percentage of Drosophilidae in the wagtail diet was not related to the numbers available, as measured by the traps (Fig. 2), but was inversely correlated with the numbers of Chironomidae caught in the traps (Fig. 3). The percentage of Chironomidae in the diet was positively correlated with the number of Chironomidae caught in the traps (Fig. 4). Therefore on days when chironomids were abundant the wagtails fed on them almost exclusively, but as numbers decreased, more and more Drosophilidae were incorporated into the diet. There were also significant correlations between the percentage of Drosophilidae (negative) and the percentage of Chironomidae (positive) in the diet and the relative abundance of chironomids in the traps, that is to say the percentage of total



Fig. 3. Relationship between the number of Chironomidae in the traps and the percentage of diet which consisted of Drosophilidae, in the yellow wagtail flock, for ten days. $r_s = -0.830$, P < 0.01.



FIG. 4. Relationship between the number of Chironomidae in the traps and the percentage of diet which consisted of Chironomidae, in the yellow wagtail flock, for ten days. $r_s = 0.843$, P < 0.01.



FIG. 5. Feeding rate of the yellow wagtail flock during ten days, mean ± 1 S.E.

trap catch which consisted of chironomids. However, these correlations disappeared when absolute abundance was partialled out. Therefore it was the absolute number of chironomids available that influenced the change in diet of the wagtails, rather than the number of chironomids relative to other prey.

During the ten days, the feeding rate of the flock birds varied from twenty-five to thirty-five items per min (Fig. 5), remarkably little considering the great changes in diet over this period. The variation in feeding rate was not associated with changes in diet nor with prey abundance (P > 0.05 in all cases). It seems possible therefore that the wagtails were adopting a certain feeding strategy, namely walking over the water surface and picking up active prey at a rate of about thirty items per min, and varying their diet to keep this strategy constant. For some unknown reason they preferred chironomids, but as the number of these decreased they incorporated more and more Drosophilidae into their diet to maintain their feeding rate.

The feeding behaviour of single wagtails

Single wagtails of both species were observed feeding on flies around dung pats. Most of my observations were made in an area of the meadow, 350×120 m, on which there were up to thirty cows and ten horses. There were about 400 dung pats in this area, approximately one every 10 m.

Dispersion

Wagtails feeding round dung pats always foraged individually, with 50–100 m between birds. Individuals wandered over wide areas of the meadow and there was no attempt to defend fixed areas, although they did defend the areas in which they were feeding at the time. If another wagtail landed nearby then a chase occurred but dispersion was probably maintained mainly by avoidance, facilitated by the wagtails' loud calls and conspicuous plumage. Birds were only aggressive while feeding and when resting and preening round the dung pats, several were often seen side by side.

Prey selection

There were five main types of prey on the dung pats; large flies of the family Scatophagidae, medium size flies of the families Sepsidae and Sphaeroceridae, small flies of the family Sphaeroceridae, and small beetles, mainly Staphilinidae (Plate 1 (a)). Although Scatophagidae were by far the most abundant prey on the dung pats, the wagtails took about equal numbers of Scatophagidae and the large Sphaeroceridae. They also took some beetles but tended to ignore the Sepsidae and small Sphaeroceridae (Table 6). There was no difference between the prey taken by pied and yellow wagtails (Mann– Whitney U-test, two-tailed, P > 0.05 for each prey), and in the following discussion the data from both species are treated together.

Whenever I approached a dung pat the Scatophagidae, large Sphaeroceridae and Sepsidae tended to run off over the surface of the pat or scatter into the surrounding grass, while the small Sphaeroceridae ran down into the cracks in the dung. Wagtails never probed into the dung but only took prey from the surface, so one of the reasons that the small Sphaeroceridae were ignored may have been that they became unavailable when disturbed. However, they may also have been rejected because they were too small and therefore unprofitable.

This explanation cannot apply to the Sepsidae, which although not very abundant were nevertheless the same size as the large Sphaeroceridae and yet were hardly ever eaten



PLATE 1. (a). The five main prey available to wagtails foraging on dung pats. No. 1–4 are adult flies (Diptera) and no. 5 is a beetle (Coleoptera). (1) Scatophagidae, (2) large Sphaeroceridae, (3) small Sphaeroceridae, (4) Sepsidae, (5) Staphilinidae. The line represents 5 mm. (b). Wing remains of prey eaten by wagtails foraging on dung pats, found in the birds' faeces. The number opposite each wing refers to the prey in (a). The line represents 5 mm. Photographs by John Haywood.

(Facing p. 44)

by wagtails. Sepsids have the abdomen basally constricted and are very ant like in appearance (Colyer & Hammond 1968). They also have scent glands which are effective against insect predators on the dung pats (Parker 1972). Therefore if these glands were also effective against avian predators, Sepsids may gain protection by being Müllerian mimics of ants. Although some species of birds eat ants (Formicidae), most species do not, apparently on account of their distastefulness (Poulsen 1956).

To test this hypothesis, live Sepsidae were presented in a dish together with the other four types of prey found on dung pats, to a captive pied wagtail. The bird immediately ate all the prey except the Sepsidae. When presented with Sepsidae alone, the wagtail showed conflict behaviour, including approaching the dish and then leaving it again, walking in a circle and bill wiping. It also showed this conflict behaviour to ants. However, after two weeks in captivity the bird would eat both Sepsids and ants, though always showing some initial hesitation. Sometimes it showed no apparent discomfort, while on other occasions it fluffed up its feathers and wiped its bill after having eaten the prey. I conclude that wagtails prefer to ignore ants and Sepsidae but will eat them sometimes, perhaps when they are hungry or have no alternative prey available (Poulsen 1956).

Table 6. Prey selection by single wagtails feeding on insects on dung pats; figures are $mean \pm 1$ S.E.

	Body Available			Eaten			
Prey	length mm	No. per 100 pat transect	% total prey	Pied Wagtail	remains in dropp Yellow Wagtail	Both combined	
Scatophagidae	5–10	399± 89	77.1 ± 4.9	35.5 ± 1.8	35.1 ± 9.2	35.3 ± 4.5	
Sphaeroceridae	1–2	44 ± 14	6.9 ± 1.4	1·6±0·9	2.3 ± 1.1	1.9 ± 0.7	
Sphaeroceridae	3-4	53 ± 19	10.1 ± 2.6	35.9 ± 5.6	41.3 ± 10.7	38.6 ± 5.9	
Sepsidae	3-4	7 ± 5	0.7 ± 0.5	0.1 ± 0.1	0.0	0.1 ± 0.1	
Coleoptera	2-3	41 ± 18	$5 \cdot 1 \pm 1 \cdot 6$	12.5 ± 3.1	6.4 ± 2.5	9.4 ± 2.1	
Others*		1 ± 1	0.1 ± 0.1	14.4 ± 4.1	14.9 ± 2.6	14.7 ± 2.6	
Total		543 ± 120	5979	779	667	1446	
No. samples		11 tra	nsects	8 days	8 days	16 days	

* Includes the following prey: Calliphoridae, Mycetophilidae, Lonchopteridae, Syrphidae, Chloropidae, Bibionidae, Chironomidae, Drosophilidae, Tipulidae, Agromyzidae, Ichneumonidae, Aphididae, Araneae.

Therefore small Sphaeroceridae were probably rejected because of their small size and Sepsidae on account of their unpalatability. To understand why the wagtails did not specialize entirely on the largest prey, the Scatophagidae, which would presumably have been the most profitable, we have to examine the feeding strategy on dung pats in more detail.

Search strategy

Scatophagidae visit dung pats in order to mate and lay eggs, and during the day very few are found away from dung (Parker 1970). Because they prefer fresh pats to old ones they are patchily distributed, and in the study area they only occurred on 37% of the pats available. Wagtails did not land on dung pats at random but tended to go to those pats which had Scatophagidae on them (Table 7, $\chi^2 = 26.4$, 1 df, P < 0.001). Scatophagidae are large flies and I could easily see them on the dung pats from 10 m away. The wagtails could also probably visually assess the presence or absence of these prey from a distance.

Some pats had only one or two Scatophagidae while others had up to sixty. Whenever a wagtail approached a pat the Scatophagidae were disturbed and quickly flew off, scattering into the surrounding grass. As they did so the wagtail made a quick grab at a prey but it often missed altogether. Table 8 shows that a wagtail was more likely to be successful if there were only one or two Scatophagidae on the pat rather than a swarm of them ($\chi^2 = 4.22$, 1 df, P < 0.05). This was presumably because the scattering of the swarm interfered with the capture strategy of the wagtail in some way, by causing a confusion effect (Humphries & Driver 1971), similar to that described for fish schools and their predators (Neill & Cullen 1974). When a wagtail was successful at capturing Scatophagidae on the pats it could usually only catch one before the others flew off. Out of forty-two occasions that a wagtail was successful in capturing at least one Scatophaga from an original swarm, it caught one on thirty-four occasions, two on six occasions and three on two occasions. Although wagtails were more successful at capturing Scatophaga when there were one or two on the pat as opposed to a swarm, nevertheless they preferred to visit pats which had swarms on them (Table 7, $\chi^2 = 7.23$, 1 df, P < 0.01).

These results suggest that wagtails were not visiting pats solely in order to catch the

Table 7. Comparison between the number of dung pats available to thewagtails on which there were Scatophagidae and the number of pats actuallyvisited by wagtails which had Scatophagidae on them

	Number of d	lung pat	S		
	with no	with \$	Scatopha	% pats with	
	Scatophagidae	1–2	>2*	Total	Scatophagidae
Available (transect counts)	948	227	338	565	37.3
Visited by wagtails	55	20	61	81	5 9·6

* This category includes three to sixty Scatophagidae, referred to in the text as a swarm.

 Table 8. Capture success of Scatophagidae on dung pats by wagtails; comparison between success at pats where there were only one or two Scatophagidae and success at those where there was a swarm

No. Scatophagidae originally on dung pat	No. of occasions at least one	wagtail caught none	% occasions successful
1–2	19	1	95∙0
>2 (swarm)	42	19	68∙9

Scatophaga, but mainly in order to disturb them into the surrounding grass. In fact very little time was spent on the pats themselves (mean ± 1 S.E. = 4.37 ± 0.34 s, n = 132) and the wagtails quickly left to search in the grass round the pat where the Scatophaga had scattered. On one occasion a wagtail carefully approached a pat and quietly picked off several Sphaeroceridae without disturbing a swarm of thirty Scatophagidae which were also on the pat but which it ignored. Therefore the sudden approach to the dung pats, which was the normal strategy of the wagtails, seemed to be an act of deliberate disturbance.

Once the prey had dispersed into the surrounding grass they were easy to capture and the wagtail was probably nearly 100% successful in its capture attempts, just as it was when capturing single Scatophaga on the pats (Table 8). However, the capture rate of these scattered Scatophaga decreased rapidly with time (Fig. 6), so that the capture rate in the first 10 s after leaving the pat was significantly greater than that from 11-20 s (t = 4.67, 75 df, P < 0.001) but there was no further change after this. The effect of the wagtail's disturbance was therefore short lived, perhaps because the Scatophaga dispersed still further afield or began to hide in the grass. Therefore there was a premium on the wagtail getting into the grass as soon as possible after disturbing the prey, and this probably explains why they spent only a few seconds on the pat itself.

Optimal foraging theory predicts that a predator should give up feeding in a patch when its feeding rate drops to the average feeding rate in that habitat (Krebs, Ryan & Charnov 1974). Because of the rapid decrease in capture rate with time, the wagtails should have stopped searching in the grass round a pat after the first 10 s and then gone on to another pat, in order to maximize feeding efficiency. The mean interval between successive pat visits for wagtails that were feeding entirely on Scatophagidae was $12\cdot8\pm2\cdot3$ s (n = 14), close to the time that would be expected if the birds were foraging optimally.

However, there were very few observations of wagtails that were specializing on Scatophagidae. Most birds picked up small items (which faeces analysis showed to be mainly the large Sphaeroceridae, Table 6) as well as Scatophagidae in the grass round the dung pats. For these birds, the mean interval between pat visits was significantly larger than that for wagtails feeding on Scatophagidae alone (mean ± 1 S.E. = 28.65 ± 3.68 s, n = 40; t = 2.46, 52 df, P < 0.02).



FIG. 6. Single wagtails feeding round dung pats, showing the decline in the rate of capture of Scatophagidae, with time after leaving the dung pat. (Mean±1 S.E.)

The few observations of wagtails which were specializing on Scatophagidae were made in areas where there was a high density of fresh dung pats and it was therefore possible for the birds to visit a pat on which there were Scatophagidae every 10–15 s, which was necessary if they were to forage optimally on this prey. However, because of the patchy distribution of Scatophagidae, in most cases the feeding strategy of the birds was probably constrained by the distance between pats. Most wagtails probably incorporated Sphaeroceridae into their diet as well as Scatophagidae because the large distance between pats meant that they were unable to forage as efficiently on Scatophagidae alone.

After the Scatophagidae had been disturbed from a pat they gradually found their way back, walking upwind through the grass, following the scent of the dung. On three occasions I managed to measure the time of the returns of Scatophagidae after they had been disturbed from a pat by wagtails (Fig. 7). In each case it took several minutes for all the flies to return. One possible feeding strategy that the wagtails could have used would have been to wait on or near the pat and catch the prey as they returned. Assuming ideal conditions, namely that the flies returned one at a time and that the wagtail was 100% successful in its capture attempts, then from Fig. 7 the average capture rate by this strategy would have been 3.6 Scatophagidae per min. On one occasion a wagtail was observed feeding in this way, and having disturbed twenty Scatophagidae from a pat it



FIG. 7. The return times of Scatophagidae, disturbed by wagtails from the dung pat at time 0. The number of Scatophagidae originally on the dung pat before disturbance is shown next to each line.



FIG. 8. Size selection by wagtails, with Scatophagidae as prey. The percentage of frequency distribution of the sizes available on the dung pats is shown in black, and the sizes of prey eaten by the wagtails is in white.

caught seven in 140 s as they returned, a rate of three per min. This capture rate is much less than that achieved by the strategy of searching in the grass round the pat and is presumably the reason why the sit and wait strategy was only observed on this one occasion.

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The influence of size on selection of Scatophagidae

Scatophagidae vary in size from 5 to 10 mm in body length, females being smaller than males. On the dung pats males outnumbered females by 3.7 to 1, a similar figure to the 4:1 ratio found by Parker (1970). There was no difference in the size of Scatophagidae eaten by pied and yellow wagtails, as measured by the length of wings in their droppings. Both species, however, took smaller sizes than would be expected from those available on the dung pats (Fig. 8, $\chi^2 = 38.77$, 4 df, P < 0.001), preferring flies about 7 mm in length. Holling (1964) has shown that praying mantids (*Hierodula crassa* Giglio-Tos) select the size of prey at which they are most efficient at handling. Similarly, finches (Fringillidae) prefer seeds of a size which they can dehusk most efficiently in terms of maximum kernel weight per unit time (Kear 1962). To test this hypothesis for the wagtails, I gave various sized Scatophagidae to a captive pied wagtail and measured the handling times, that is the times from picking up the prey to swallowing it. Small Scatophagidae, 5 mm in length, were swallowed immediately, often in less than a second, whereas large ones, 10 mm in length, were bashed against a perch, sometimes dropped and took 5–10 s to handle. From calorific values (Bryant 1973) and the handling times for



FIG. 9. The energy intake per unit handling time of different size Scatophagidae by a captive pied wagtail.

each size of prey, the energy intake per unit handling time was calculated (Fig. 9). It can be seen that, just as with Holling's mantids, the size of prey selected by wild wagtails corresponds to the optimum prey size they can handle.

Thus at one end of the size scale small prey 1–2 mm long, such as the small Sphaeroceridae, were ignored because although quick to handle they were not worth very much energy, while at the other end of the scale the largest Scatophagidae were rejected because although worth a lot of energy they took too long to handle. In support of this idea, on three occasions wild wagtails were seen to catch Scatophagidae on dung pats and then drop them and ignore them. These three flies were all large ones, 10 mm long. The feeding strategy adopted by the wagtails on the dung pats, involving rapid pat visits with a premium for getting into the surrounding grass as quickly as possible, probably means that it is more profitable for them to ignore these large flies, because of their disproportionately long handling times.

Feeding techniques

Single wagtails used a greater variety of feeding techniques and also fed at a slower rate than the flock birds (Table 9, compare with Table 4). Comparing the two species of

wagtails, pied wagtails used more run-picking (Table 9, $\chi^2 = 5.79$, 1 df, P < 0.05) and more fly-catching ($\chi^2 = 15.63$, 1 df, P < 0.001) than yellow wagtails, but there was no difference in feeding rates (t = 0.96, 54 df, P > 0.2). The tail appears to assist balance when wagtails use the run-picking and fly-catching techniques and it is especially important when the birds turn rapidly in mid-air when chasing prey. In this context it is interesting to note that pied wagtails have longer tails than yellow wagtails, and grey wagtails which capture most of their prey by fly-catching (personal observations and L. Schifferli, personal communication) have the longest tail of all.

Wagtails used different feeding techniques for different prey and used more run-picking and fly-catching for Scatophagidae than they did for Sphaeroceridae, which were mainly caught by the picking technique (Table 10, $\chi^2 = 115.3$, 2 df, P < 0.001). Scatophagidae are much more active flies than Sphaeroceridae and probably require more energetic methods for capture. They are also larger and worth more in terms of energy gain, so it is profitable for wagtails to use high energy cost feeding techniques to capture them.

Table 9. Feeding techniques and feeding rates of single wagtails on dung pats

	Pied Wagtails	Yellow Wagtails
Feeding techniques		
% picking	67.4	83.8
% run-picking	13.6	8.7
% fly-catching	19.0	7.5
Total capture attempts	898	173
Feeding rates items per min		
mean ± 1 S.E.	10.1 ± 0.6	8.7 ± 1.1
(no. observation periods)	(45)	(11)

 Table 10. Feeding techniques used by single wagtails in relation to the type of prey captured

Feeding technique	Prey			
	Scatophagidae	Sphaeroceridae		
% picking	31.9	73.8		
% run-picking	39.7	9.5		
% fly-catching	28.4	16.7		
Total capture attempts	141	725		

Changes from feeding in flocks to feeding as singles

Although flock birds and singles used very different foraging strategies, wagtails often changed rapidly from one to the other. These changes were studied in two situations.

Yellow wagtails

When the yellow wagtails first arrived on the meadow in April they fed in flocks, but after two weeks the flocks had disbanded and all the birds foraged singly. During this change in social behaviour, on some days small groups of birds fed on chironomids in the grass between the dung pats but they rarely visited the pats and usually walked right past and ignored large swarms of Scatophagidae. At the same time, often only a few metres away, single wagtails visited dung pats and exploited the flies on them.

Yellow wagtails migrate in flocks (Smith 1950) and the flocking behaviour when they first arrived may have been a continuation of behaviour connected with migration.

Flocking probably acted as a constraint on the feeding behaviour of the birds because in order to maintain the flock structure all the individuals have to adopt similar foraging patterns. This was possible when the birds were feeding on an abundant source of easily captured prey such as the chironomids, but flocking was probably incompatible with feeding on dung flies which were patchily distributed and required a variety of feeding techniques for efficient exploitation. Foraging on dung flies is also liable to interference from neighbouring birds and the large individual distances necessary for this strategy would conflict with the need to maintain flock structure. Therefore when they first arrived, the migratory flocking behaviour of wagtails probably restricted the foraging strategy they could employ.

During the gradual change from flocking to solitary feeding there were superimposed diurnal changes in feeding behaviour. These changes were studied in 1974 when flock birds fed round the flooded part of the meadow in the morning and evening, but split up in the middle of the day to forage as singles round the dung pats. There was a corresponding diurnal change in the number of prey available on the dung pats (Fig. 10) with



Fig. 10. Diurnal changes in the number of prey available on dung pats. Mean ± 1 S.E. per 100 pats, for seven days transect counts.

very few prey in the early morning, a build up to a peak in the middle of the day and then a decrease again in the evening. Table 11 shows that the yellow wagtails' change to dung pat foraging in the middle of the day was a profitable one in terms of energy gain per unit time. However, in the morning and evening the decrease in the flies on the dung pats presumably meant that the flooded pool was the better place to feed.

In order to make these changes in feeding strategy the birds not only changed the place where they were feeding and the type of prey captured, but also their social behaviour. Changes were very rapid and birds which had been chasing others and maintaining individual distances of 50–100 m during the day on the dung pats, were seen feeding side by side with other wagtails in the evening, often less than 1 m from neighbours. On one occasion two birds were seen chasing each other round the dung piles and 5 min later both flew to the flooded pool to join the flock and fed side by side without any aggression.

The solitary behaviour needed for dung pat foraging meant that the increase in

profitability of feeding was at the expense of maintaining the migratory flock. In the evening and early morning the flocking behaviour was resumed presumably because the efficient exploitation of prey round the flooded pool was not incompatible with the flocking strategy.

Pied wagtails

Pied wagtails also showed rapid changes from foraging in flocks to foraging as singles. In March and April 1975 there were vast numbers of chironomids on a flooded part of the meadow and up to sixty pied wagtails fed there. The flock lacked the organized structure of the migrant yellow wagtail flocks and was probably just an accumulation of individual birds feeding together because of the localized nature of the food supply. Because of the high feeding rate birds did not interfere with each other and tolerated neighbours less than 1 m away. The main factor limiting feeding rate, which remained constant over this period at over seventy items per min, was probably the rate at which the wagtails could pick up the prey. During this time, some birds also foraged round dung pats.

On twenty-five days I counted the number of wagtails feeding in each situation at 13.00-14.00 hours G.M.T. each day, when there were the peak numbers of flies on the

 Table 11. The energy intake per unit time from feeding round a flooded pool

 compared with feeding round dung pats, during the middle of the day when

 there were peak numbers of prev on the dung pats

	Yellow Wagtails May 1974		Pied Wagtails March 1975		
	Pool	Dung pats	Pool	Dung pats	
Feeding rate items per min	29.1	8.7	73.2	10.1	
Mean calories per item	1.6	7.8	1.6	7.8	
Energy intake, cal per min	46.6	67·9	117.1	78.8	

dung pats (Fig. 10). Counts were also made of the number of flies during a transect of 100 pats. On some days, especially when it was cold, there were very few flies present, while on other days, there were several hundred. Sometimes there were large numbers of both Scatophagidae and Sphaeroceridae, but on other days only one of these were abundant.

Single birds often left the pool and flew over to an area of dung pats, sometimes landing and remaining to feed, and on other occasions returning to the pool after a minute or two. It is possible that the wagtails were visually assessing the number of flies on the pats during these short excursions. Figure 11 shows that the wagtails tended to switch from feeding round the pool to dung pats when there were greater than 150 Scatophagidae per 100 pat transect, but also provided that there were large numbers of Sphaeroceridae present as well. On days when there were large numbers of one of these prey only, most of the wagtails remained round the flooded pool to feed. This suggests that both types of prey were needed for dung pat foraging to be worthwhile and, as described above, this may have been due to the patchy distribution of the Scatophagidae.

It may be expected that, just as the yellow wagtails changed strategy to increase feeding efficiency, so the pied wagtails changed to dung pat feeding to increase energy intake per unit time. From Fig. 11, I would predict that dung pat foraging became more efficient than chironomid foraging round the flooded pool when the number of Scato-

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phagidae exceeded 150 per 100 pats, and there were Sphaeroceridae present as well. However, for pied wagtails, the energy intake per unit time on the dung pats was always less than that from feeding round the flooded pool (Table 11). Therefore the birds were apparently switching to dung pats to their loss in terms of energy intake.



FIG. 11. The percentage of number of pied wagtails on the meadow that were feeding round the dung pats, as opposed to round the flooded pools, in relation to the number of Scatophagidae present on the dung pats. Counts on 25 days. • Days when there were greater than fifty Sphaeroceridae, \circ days when there were less than twenty Sphaeroceridae per 100 pat transect count.

DISCUSSION

Solitary or flock feeding?

It has been appreciated for some time that food is one of the main factors influencing social behaviour (Crook 1965; Kummer 1971) and this study shows that changes in social behaviour may be very rapid in response to changes in the food exploited (see also Kruuk 1972; Davies 1976).

When foraging on insects on dung pats the wagtails fed solitarily, probably to avoid interference from other individuals. This feeding strategy involved hunting over large areas of the meadow because the prey was both patchy and liable to disturbance by the birds, so that they could not feed in the same area again until the prey had reassembled on the pat. Dung flies prefer fresh pats (Parker 1970) and therefore the available food supply changed so that areas which were good on one day were not necessarily good the next day. Therefore it would probably have been uneconomical for the birds to defend permanent territories, which they did in other situations where feeding was predictably good (Davies 1976). The social strategy adopted instead was that of temporary territories where the wagtails only defended those areas in which they were feeding at the time. Similar behaviour has been described for reed warblers (Acrocephalus scirpaceus (Herm.)) (Davies & Green 1976) where avoidance of interference between foraging birds was also the main reason for the spacing behaviour. Leyhausen (1965) and Eaton (1970) have described analogous situations in domestic cats and cheetahs (Acinonyx jubatus Schreber), neither of which can economically defend the large areas needed for hunting. In these cases temporal separation by avoidance was mediated by scent marking, whereas in the wagtails the loud calls and conspicuous plumage brought about the same result.

In some cases flocking behaviour may increase the efficiency of food exploitation (Krebs *et al.* 1972; Ward & Zahavi 1973; Cody 1971), and this may also apply to the wagtail flocks although there is no direct evidence. However, flocking may also be concerned with other activities, such as predator avoidance (Wilson 1975). Goss-Custard (1970, 1976) has shown that in waders (Charadrii) compact flocks may reduce the risk of predation, but be incompatible with efficient feeding because of interference between foraging individuals. The flock formation adopted may be a compromise between these two selective pressures. Similarly the yellow wagtail flocking behaviour when they first arrived, perhaps connected migration, constrained their feeding strategy so that they could not change to dung pat feeding even though this may have increased energy intake per unit time foraging. When the flocks disbanded at the end of the migration period, the birds were released from this constraint and in fact changed their feeding strategy during the day to maximize energy intake.

Where to feed?

Within the habitats in which an animal feeds there will be considerable heterogeneity. Wagtails feed in grassland and farmland but within these there are many types of feeding patches, such as dung pats and flooded pools. One of the criteria that birds use when choosing patches is energy gain per unit effort or profitability (Royama 1970; Tullock 1971; Smith & Sweatman 1974). In this study, the yellow wagtails made diurnal changes in feeding site consistent with this view. The transition to independent feeding in young spotted flycatchers can also be interpreted as a decision by the young between two feeding strategies, either begging for food from the parents or capturing prey themselves, made on the basis of energy intake per unit effort (Davies 1977).

However, the pied wagtails in this study showed changes in feeding site which resulted in a decrease in energy intake. We must conclude that either they were not feeding optimally or were choosing food patches on some other criterion. The latter seems the more likely and it may be misleading to expect birds always to maximize energy gain. For example, they also need specific nutrients (e.g. MacLean 1974) and the pied wagtails may have changed to dung pat foraging in order to vary their diet. Alternatively the dung pats may have been more suitable for some other activity, such as searching for mates, which offset the disadvantage of a decrease in energy intake.

In another situation, some pied wagtails spent time defending permanent winter territories even at times when flock birds nearby were doing better in terms of energy gain (Davies 1976). Therefore on the short term view these birds were at a disadvantage. But throughout the whole winter they were probably at an advantage because these territories were the best places to feed on hard days when there was snow on the ground and food was very scarce. Thus it may be more appropriate to examine a bird's behaviour in terms of optimization in the long term rather than by examining day to day or diurnal changes (Katz 1974).

How to exploit food patches?

For predators feeding on cryptic, stationary prey, the ability to detect the prey may be the most important factor limiting the feeding rate, and such predators may adopt a 'search image' in the sense that they learn, with experience, to detect the crypsis (Krebs 1973). When feeding on dead insects, wagtails may use prey shape or colour as searching cues (Davies 1976). However, when feeding on live, mobile prey the activity and ease of capture are also likely to influence prey selection (Hespenheide 1975). The relative importance of crypsis and capturability may vary with the activity of the prey (Davies & Green 1976).

The yellow wagtail flock probably used prey activity as a searching cue and selected the most visible prey. It is not known what individual wagtails were eating, but because all the birds used the same feeding techniques and fed at the same rate, it is likely that all the members of the flock were taking the same prey. Murton (1971) has shown that in order to remain in a flock, woodpigeons (*Columba palumbus* L.) must peck at the same rate as other individuals. He suggested that they copied each other's pecking movements and this resulted in the flock tending to favour a particular prey type. In the yellow wagtail flock the need to maintain flock structure also seemed to constrain the feeding behaviour of individuals birds. The simplest way to remain in a close knit group may be for all individuals to move and peck at the same rate, and this may explain why they all foraged in exactly the same way and varied the diet to keep the feeding strategy constant. Single wagtails were not so constrained but pursued particular prey varying the feeding technique as appropriate.

The diet of the yellow wagtail flock was influenced by the absolute abundance of their preferred prey, the Chironomidae, and as the numbers of these decreased, more and more Drosophilidae were incorporated into the diet. The relative abundance of the prey was not important, which contrasts with some situations reviewed by Murdoch & Oaten (1975) where predators switched to exert disproportionately heavy predation on the prey of greatest relative abundance. A predator's diet may be influenced by relative abundance only at high prey densities, where it may be more efficient to concentrate on one prey at a time because of visual searching efficiency (Dawkins 1971), efficiency in prey capture (it may be more efficient to use a sequence of the same feeding techniques) or digestive efficiency (Spitzer 1972). At low prey densities a variety of prey may be accepted to ensure a sufficient feeding rate.

The dung pat situation, although relatively simple, with only five types of prey available to the wagtail predator, illustrates how complex the factors influencing prey selection may be. Two of the prey (small Sphaeroceridae and Staphilinidae) were small and probably unprofitable as a food source and one of the prey (Sepsidae) was distasteful. The largest prey available (Scatophagidae) were difficult to catch when they occurred as swarms on the dung pats and the ability of the wagtails in handling large prey restricted the size of Scatophagidae that they captured. Furthermore the prey occurred in patches. First, the wagtails had the problem of finding these patches, which they could do visually because the Scatophagidae were large and conspicuous. Secondly, they had to decide when to leave a patch and go to the next one, in which they behaved as predicted by optimal foraging theory (Krebs et al. 1974). Probably because there was often a large distance between patches and perhaps also because of the difficulty in capturing the Scatophagidae, the wagtails also incorporated the next largest prey (the large Sphaeroceridae) into their diet. Finally there were diurnal and day to day fluctuations in the prey available on dung pats, so that sometimes the wagtails had to switch to a different feeding strategy altogether.

In conclusion, wagtails exhibited rapid changes in social behaviour, feeding site and the type of prey eaten. Sometimes these changes resulted in maximization of energy intake. However, on other occasions wagtails did not forage optimally by this criterion probably because of the need to engage in other activities, whose performance conflicted with feeding considered in terms of energy gain.

Feeding behaviour of wagtails

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SUMMARY

(1) The feeding behaviour of pied and yellow wagtails, small insectivorous birds, was studied on a meadow near Oxford, to examine the problems facing predators when searching for their food: Solitary or flock feeding? Where to feed? How to exploit food patches? Prey taken (mainly adult Diptera) was determined by examination of wing remains in the birds' faeces.

(2) Flocks of wagtails were studied feeding on insects on the water surface of flooded pools. Changes in their diet over ten days were related to changes in the absolute abundance of the preferred prey (Chironomidae) and as the numbers of these decreased, more of the alternative prey (Drosophilidae) were incorporated into the diet to maintain the feeding rate. A constant feeding rate, with all individuals foraging in the same way, may have been the mechanism by which flock structure was maintained.

(3) Solitary wagtails were observed exploiting insects on dung pats, where there were five main prey. The smallest (Staphilinidae and small Sphaeroceridae) were rejected and one (Sepsidae) was distasteful. The largest (Scatophagidae) were patchily distributed and difficult to capture when in swarms and so the next largest prey (large Sphaeroceridae) were also incorporated into the diet. The size range of Scatophagidae eaten corresponded to the optimum in terms of energy intake per unit handling time. The birds' behaviour in leaving patches was as predicted by optimal foraging theory.

(4) Despite the great differences in social behaviour and prey eaten at the two feeding sites, wagtails switched rapidly from one to the other. Sometimes these switches resulted in maximization of energy intake but on other occasions they did not, probably because the need to engage in other activities constrained feeding efficiency considered in terms of energy gain.

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