PARENTAL CARE OF FLEDGED YOUNG, DIVISION OF LABOR, AND THE DEVELOPMENT OF FORAGING TECHNIQUES IN THE NORTHERN WHEATEAR (*OENANTHE OENANTHE* L.)

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ABSTRACT.—The care of fledged young by parents and the interactions between parents and young were studied in seven broods of Northern Wheatears (*Oenanthe oenanthe* L.) in an agricultural area near Uppsala, central Sweden. Time budgets of young and the development of foraging skills were also quantified. Young of the same brood were observed out of the nestholes on the 15th or 16th day after hatching. The parents did not divide the brood until day 3 or 4, day 1 being the 16th day after hatching (assuming that all young fledged on the 15th day). Full stability of family units, with no transfers of responsibility for feeding specific young, was achieved on days 3–8. Both parents fed their respective groups of young at different sites, and young of the same family unit appeared to be aggregated in the territories. They perched nearer to each other on average than to young fed by the other parent. These results support the hypothesis that a division of labor in altricial birds has evolved to allow parents to locate their young more easily and to reduce travel distances between sites at which prey are captured and the locations of young.

Young wheatears depended on their parents for 2 weeks after leaving the nest. During that time, they became more active and mobile, spent less time calling and waiting for the parents to feed them, chased their parents more intensively to obtain food, and spent more time foraging. The marked increase in the chasing frequency of young after the first week coincided with a marked decrease in parental feeding rates and in the responsiveness of the parents to the begging calls of the young. Young also greatly increased their foraging activity after day 10, when parental feeding rates dropped to very low levels. These data support the hypothesis that parental reluctance to feed the young determines the onset of fledgling independence. Rates at which young attempted to capture prey and the proportion of successful attacks increased with age. Foraging techniques that are more dependent on flight performance (aerial hawking, perch-to-ground sallying) appeared later and were used less by the young than was ground-gleaning. There was a negative relationship between the intensity of chasing by the young and their capture success rates during different hours, which suggests that they switched between chasing the parents and self-feeding, depending on which was the most profitable strategy at the moment. *Received 4 November 1983, accepted 12 April 1984.*

PARENTAL care in altricial birds has been studied mainly during the nestling period, as it is often difficult to observe young after they have left the nest. In most passerine birds, however, parental care continues after the young leave the nest. The length of this period varies in different species and can be twice as long as the period of feeding nestlings (Skutch 1976). Few quantitative studies have dealt with parental feeding of fledglings (but see Davies 1976, Smith 1978, Smith and Merkt 1980), although parental investment after the young leave the nest has been suggested to be even greater than during the nestling stage (Royama 1966, Drent and Daan 1980).

A division of labor between the parents when feeding fledged young, each parent feeding only certain individuals of the brood, has been reported in several studies of passerines (Snow 1958, Nolan 1978, Smith 1978). Smith (1978) suggested that labor division would be an advantage in that it would help the parents to locate young and would lead to a reduction in parental travel times and, therefore, in energy expenditure. For this advantage to occur, the division of labor should be accompanied by the spatial separation of the two groups of young in different parts of the territory. In this field study of Northern Wheatears (*Oenanthe oenanthe* L.) feeding fledged young, I have looked at

the location of young in the territories and at
the distribution of parental feedings among dif-
ferent young.

The length of the period of fledgling care is
probably determined by the development of
foraging techniques by the young (Davies and
Green 1976) and by the interaction between
offspring and parents (Davies 1976). Davies
(1978) experimentally showed that "parental
meanness" in feeding the young determined
the onset of offspring independence. I examine
both the changes in the interaction between
parents and fledged young and the develop-
ment of foraging skills with age of the young,
and I compare changes in both processes.

METHODS

One brood of 7, two broods of 6, and one brood of
5 nestling wheatears were color-banded and fol-
lowed for 20 days after they had left the nest in June
and July 1982. The habitat was open meadowland
near Uppsala in central Sweden (59°50′N, 17°40′E).
These broods were reduced to 5 (brood I), 6 (II), 4
(III), and 3 (IV) young, respectively, shortly after the
first young left the nest. Territories I and II, II and
III, and III and IV were adjoining and covered areas
of 1–1.5 ha. I observed parental feedings and the be-
havior of young from 20–80 m away (mostly from
40–50 m) with binoculars (10×) or telescope (40×)
and dictated events continuously into a tape recorder
as they occurred. I played the tapes back later while
observing a running stopwatch to determine the time
spent in each activity. When a bird was lost from
sight, the series of observations was stopped. The
following data were recorded: individual; time of day;
location (on a map of the territory); whether the bird
was resting, preening, silent, or calling; whether it
was feeding, flying alone, flying after one of the par-
ents, or being fed by parents; the type and success of
prey-capture attempts; and interactions between
young of the same or different broods. All observa-
tions were made between 0500 and 1200 local time.

Because I did not obtain sufficient data to show
changes in the behavior of each individual with age,
data for young of the same age were pooled. The age
of the young is expressed as days after leaving the
nest, with day 1 being the 16th day after hatching
for all young. I have assumed that all young fledged
on the 15th day, which was the earliest age at which
young were observed outside of the nestholes. The
actual date of leaving the nest is difficult to deter-
mine with certainty, as young usually stay in the
stone pile of the nest for long periods until their 18th
day. That young of broods II, III, and IV were first
seen outside on the 16th day could be due to the brief
observation times for these broods before that day.

Data on the distribution of parental feedings, spatial
separation of young, and interactions between young
refer to the whole study period, unless I state oth-
erwise. Data presented are grouped for age intervals
of 2 days, to reduce variation due to unequal daily
observation times.

In addition to these intensive observations of 4
broods, I also recorded parental feedings of 2 broods
of 5 (V and VI) and 1 brood of 4 (VII) color-banded
fledglings in the same study area in 1983 during 1
week. I noted parental feedings of different young,
locations where the young were fed, and distances
between these locations. Observations of these three
broods covered days 2–10.

Spatial overlaps in distribution (α) were calculated
by the formula

$$\alpha = 1 - \tfrac{1}{2} \sum_i |(p_{xi} - p_{yi})|,$$

where p_{xi} and p_{yi} are the proportions of feedings of
or by individuals x and y on site i. For the three
broods in 1983, I used the proportion of time spent
on different feeding sites instead of the proportion
of visits to calculate spatial overlaps.

RESULTS

Division of labor by the parents.—The young
were first observed out of the nestholes, which
were always situated in stone piles, on the 15th
(brood I) or 16th day after hatching (territories
II–IV were only briefly checked daily before
that date). In brood I, the heaviest young came
out first [the 4 young observed outside on the
15th day weighed an average of 24.4 g ± 1.5
(SD) the day before, while the 3 remaining
young weighed only 17.7 g ± 4.5 on average].
During the first days after fledging, 2 young of
brood I (2 runts, 1 of which was not observed
outside at all), 1 of brood III, and 1 of brood IV
died in the nest pile, probably of starvation.
These young were always the lightest of their
respective broods. A high proportion (42.3%)
of the feedings to brood I on the 15th day were
delivered outside the nesthole. The largest sib-
lings appeared to be obtaining most of the food
deliveries outside or at the nest entrance. The
days directly after the first young fledge thus
seem to be a critical period for the small indi-
viduals of each brood. All the studied individ-
uals had come out of the nesthole by the 16th
day after hatching (day 1). On days 3–4, they
started to move to a few nearby stone piles,
usually 10–50 m from the nest. After day 5 the

TABLE 1.   Number of food deliveries to individual young in seven wheatear broods and tests of independence of distributions of feedings by the two parents of each brood. Individual E of brood I disappeared after day 5.

| Brood | Feeding parent | Young | | | | | | Tests of independence of feeding distributions |
		A	B	C	D	E	F	
I	Male	13	24	3	4	10	—	$\chi^2 = 56.8$, 4 df, $P < 0.001$
	Female	4	2	34	19	9	—	
II	Male	22	41	10	4	1	0	$\chi^2 = 91.5$, 5 df, $P < 0.001$
	Female	2	0	8	10	13	22	
III	Male	5	8	0	0	—	—	$G = 39.9$, 3 df, $P < 0.001$
	Female	0	0	4	12	—	—	
IV	Male	3	4	2	—	—	—	$G = 5.6$, 2 df, $P > 0.05$
	Female	0	3	5	—	—	—	
V	Male	12	7	1	0	0	—	$G = 43.32$, 4 df, $P < 0.001$
	Female	0	0	0	6	12	—	
VI	Male	14	9	1	0	0	—	$G = 53.10$, 4 df, $P < 0.001$
	Female	2	0	0	13	8	—	
VII	Male	9	2	2	0	—	—	$G = 16.53$, 3 df, $P < 0.001$
	Female	0	1	2	4	—	—	

young were found increasingly scattered throughout their entire territory.

Already on days 1–5, both parents of the two broods for which there were sufficient data for the first days were feeding certain individual young more intensively (test of independence of distribution of parental feedings: $\chi^2 = 17.1$, 4 df, $P < 0.01$, $n = 76$ for brood I; $\chi^2 = 51.3$, 5 df, $P < 0.001$, $n = 73$ for brood II). The division of labor appeared to commence after day 3 for some pairs, however. On day 3 the first young left the immediate vicinity of the nest. For brood I, there were sufficient data for days 0 (only 4 young had left the nest that day) and 3 to indicate no significant differences in the distribution of parental feedings to the individual young on these days ($\chi^2 = 0.9$, 3 df, $P > 0.05$, $n = 67$ for day 1; $\chi^2 = 1.2$, 1 df, $P > 0.05$, $n = 34$ for day 3). For brood II, also, there appeared to be no family division during the first 3 days after the young left the nest ($\chi^2 = 1.08$, 1 df, $P > 0.05$, $n = 42$ for all 3 days together).

Over the whole study period, all pairs except pair IV divided the labor between parents (Table 1). Data for brood IV, however, are too few to allow any conclusions to be drawn. The brood of 6 (II) was split evenly between the parents; In the three broods of 5, the male fed 3 and the female 2 young; the two broods of 4 were divided evenly (in brood I only after young E disappeared on day 5). Young that apparently

were fed equally by both parents (E in brood I and C in II, Table 1) were the heaviest in their respective broods and were more mobile than their siblings during the first 5 days, during which most (C) or all data (E) on parental feedings of these two young were collected. After day 5, C was fed only by the male. Complete division of the brood into two family units (i.e. the young being fed exclusively by one or the other parent) started in some broods on day 3 (broods III and V), whereas in others it started on day 6 (broods I and VI) or 8 (broods II and VII). The young responded to the division of labor by the parents by begging from and chasing the feeding parent. Only 5% ($n = 119$) of all observed chases were directed toward the other parent, and in no case did these chases end with the young in question being fed. Of the chases made after division was complete only 2.1% ($n = 93$) were directed toward wrong parent.

Spatial distribution of young.—The young were usually fed on certain elevated places (henceforth to be called feeding sites), like stone piles or large stones, for 1 week after leaving the nest. During the second week they became highly mobile (Table 2) and followed their parents around. The feeding sites used by the two parents during the whole period were significantly different for pair I ($\chi^2 = 10.7$, 4 df, $P < 0.05$), pair II ($\chi^2 = 50.7$, 7 df, $P < 0.001$), pair

TABLE 2. Two indices of the mobility of young during the first and second weeks after leaving the nest and tests of differences between weeks. The sample sizes of daily records of numbers of feeding sites are given in parentheses.

	Days 1–7	Days 8–14	Mann-Whitney U-test
Mean number of sites where each young was fed daily	2.14 ± 1.47 (79)	4.58 ± 2.94 (64)	$U = 1,146$, $P < 0.001$
Mean number of sites where each parent fed their young daily	1.77 ± 0.50 (30)	3.42 ± 2.40 (26)	$U = 255$, $P < 0.001$

III (Fisher test, $P < 0.001$), pair IV (Fisher test, $P < 0.001$), pair V (Fisher test, $P < 0.05$), pair VI ($\chi^2 = 17.6$, 2 df, $P < 0.001$), and pair VII ($\chi^2 = 46.8$, 2 df, $P < 0.001$). Although individual parents sometimes changed their main feeding sites from day to day, the members of a pair seemed to avoid feeding young at the same sites during the same day. On one occasion, both members of pair I switched main feeding site and feeding area from one day to the next, but they still remained in different parts of the territory. The separation of feeding sites used by members of pairs I and II was more marked during the first days of labor division (days 4–7 for pair I and 3–7 for pair II) than afterwards, as is shown by the overlap values of feeding places of 0.52 and 0.76 for

pair I and 0.06 and 0.42 for pair II for the early and late periods, respectively.

The division of the broods and the separation of feeding sites between parents were accompanied by a spatial separation of fledglings fed by each parent (Table 3). The visits of young of different family units to different feeding sites were significantly different for brood I ($\chi^2 = 41.9$, 8 df, $P < 0.001$), brood II ($\chi^2 = 94.5$, 9 df, $P < 0.001$) and brood III ($\chi^2 = 98.2$, 5 df, $P < 0.001$). The spatial overlap values (α) between different members of a brood were higher for young fed by the same parent than for those fed by different parents (Table 3). This pattern of spatial separation was prevalent up to day 20, when I finished my observations. The association of young on the same feeding

TABLE 3. Mean (±SD) overlap values of distributions of feeding sites calculated by the percentage of similarity index (α, formula in text), and average distance between siblings (±SD) fed by the same and by different parents in the six broods in which labor division between the parents was observed. Tests of significance of differences are Mann-Whitney U-tests. For estimates of daily distances between siblings see text.

Brood	Overlap of distributions of feeding sites visited by siblings		Average (±SD) distance (m) between siblings		Tests of significance of differences
	Fed by same parent	Fed by different parents	Fed by same parent	Fed by different parents	
I	0.84 ± 0.08	0.69 ± 0.08	16.41 ± 26.45 ($n = 22$)	42.44 ± 38.74 ($n = 43$)	$U = 812, P < 0.01$
II	0.68 ± 0.12	0.50 ± 0.11	34.57 ± 32.54 ($n = 51$)	64.03 ± 29.34 ($n = 80$)	$U = 4,258, P < 0.001$
III	0.67 ± 0.11	0.03 ± 0.07	5.00 ± 14.14 ($n = 8$)	65.38 ± 38.15 ($n = 13$)	$U = 129, P < 0.001$
V	0.83 ± 0.06	0.15 ± 0.11	22.56 ± 48.40 ($n = 16$)	122.83 ± 68.42 ($n = 24$)	$U = 363, P < 0.001$
VI	0.88 ± 0.06	0.57 ± 0.10	6.67 ± 15.57 ($n = 12$)	82.06 ± 38.65 ($n = 17$)	$U = 198, P < 0.001$
VII	0.33 ± 0.47	0.33 ± 0.32	62.00 ± 63.80 ($n = 5$)	62.00 ± 81.35 ($n = 10$)	$U = 23, NS$

TABLE 4.   Changes with age of young in (a) the proportion of observations (a new observation commences after each displacement of a young longer than 5 m) in which fledged young were associated with (less than 1 m from) a sibling (number of observations in parentheses), (b) the proportion of total observation time spent interacting with other young (mostly with siblings) (minutes of observation time in parentheses), and (c) the proportion of interactive time spent in aggressive actions against other young (attacks, chases).

Age	Proportion of observations of young in association with a sibling	Proportion of time spent in active interaction with other young	Proportion of interactive time spent in aggressive actions
Days 1–3	1.00	0.007 (195.9)	0.25
Days 4–6	0.64 (163)	0.021 (182.3)	0.12
Days 7–9	0.55 (337)	0.010 (331.6)	0.50
Days 10–12	0.41 (163)	0.026 (207.5)	0.90
Days 13–15	0.36 (147)	0.002 (215.8)	0.67
Days 16–18	0.29 (48)	0.027 (62.5)	1.00
Days 19–20	0.27 (22)	0.000 (29.9)	—

site provides the same picture. Young fed by the same parent were more often seen sitting together after day 3 than young fed by different parents (181 intra-unit associations and 71

inter-unit associations observed for broods I, II, and III; Binomial test, $P < 0.001$). The tendency to associate with their siblings decreased as young became increasingly independent of their parents (Table 4).

Young of the same group also appeared to be spatially aggregated in the territories. The average distance between siblings fed by different parents was significantly greater than the distance between young fed by the same parent except for brood VI (Table 3). I have estimated daily distances between siblings as the distances between the sites that each young visited most often (broods I–III) or between the places at which each remained most of the time during each day (the less intensively observed broods V–VII). The average distance between siblings increased with age for broods I and II from 15.5 and 27.9 m during the first week to 50.4 and 54.5 m, respectively, during the second week after fledging ($U = 7.78$, $P < 0.05$ for brood I; $U = 30.01$, $P < 0.001$ for brood II). The increasing mobility of the young led to a higher overlap between the feeding areas of different broods. The changes with age in the proportion of time spent by young in neighboring territories were calculated for broods I and II, which had adjacent territories. The proportions increased from 0.06 for brood I and 0.03 for both broods combined before day 11 to 0.27
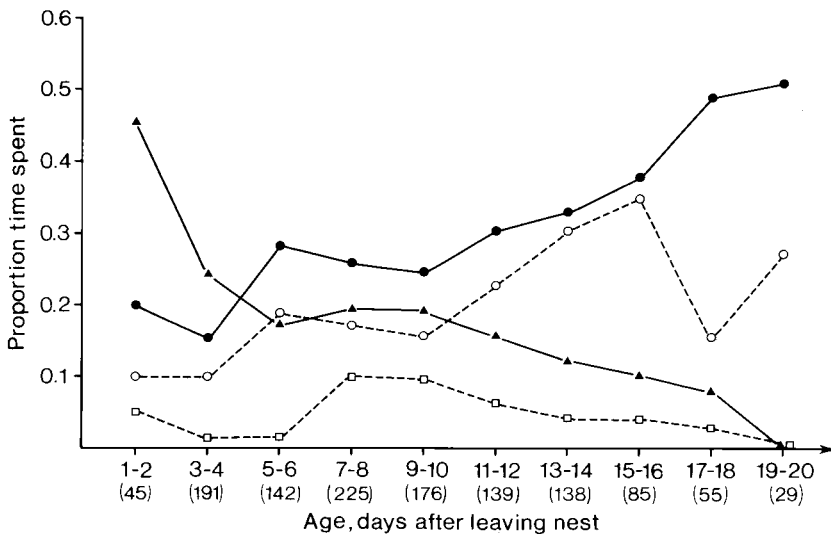

Fig. 1.   Changes with age in the proportion of observation time spent by young wheatears resting or preening without calling (●), emitting begging calls while resting (▲), foraging (○), and flying (□). Minutes of total observation time are given in parentheses on the age-axis. Data are presented for age intervals of 2 days.
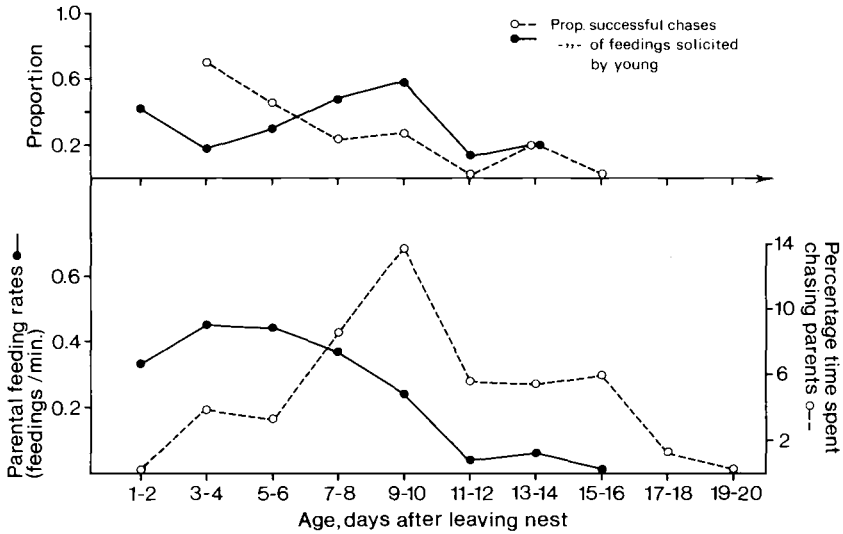
Fig. 2. Lower graph: Changes in parental feeding rates with age of young (feedings/min observation time) (left axis) and in the proportion of observation time spent by the young chasing their parents (right axis). Upper graph: Changes with age of young in the proportion of chases that were successful, i.e. were directly followed by a parental feeding, and in the proportion of feedings by parents that were solicited by young, i.e. preceded by a chase or a begging episode. Data are given for age intervals of 2 days. Minutes of observation time as in Fig. 1.

and 0.13, respectively, from day 11 onwards. These proportions are significantly different (test for differences between proportions, $z = 21$, $P = 0.001$).

Interactions between parents and young.—During the first week, the young remained near a stone pile where they could hide in case of danger. They spent most of the time resting, preening, or emitting begging calls when hungry (Fig. 1). Feeding rates by the parents were very high until day 6, after which they started to decline ($r_s = -0.83$, $P < 0.01$, $n = 8$) (Fig. 2). Some time was spent by the young in exploratory activity in the grass or between stones, where they pecked at and manipulated different, mostly inedible, objects (Fig. 3). Sometimes the young moved to other stone piles, flew toward the approaching parents, or even followed or chased parents for some distance while emitting begging calls (Figs. 1 and 2).

After day 6 there was a marked increase in the proportion of time spent by the young in chasing their parents around the territory while the parents were foraging (Fig. 2). The parents also tended increasingly to feed only young that were either calling near them or that were actively following them and begging (Fig. 2). The proportion of chases that were directly followed by feedings decreased with age of young ($r_s = -0.88$, $P < 0.05$, $n = 7$) (Fig. 2).

From day 10 onwards, the young reduced their chasing activity (Fig. 2), while spending less time calling for food and more time actively foraging (Fig. 1). The proportion of time spent in flight was highest on days 7–10 because of the intense chasing of the parents. After day 10, the parents became more and more reluctant to feed the young, as is shown by their drastically reduced feeding rates and the lower proportion of successful chases (Fig. 2). The parents often moved away from the young when they landed nearby and gave begging calls. The flight activity of the young also decreased to the level of the first week (Fig. 1). When resting, the young began to call less and less often (Fig. 1). After day 14 no more feedings by the parents were observed, but still the young continued to chase their parents, although with decreasing intensity (Fig. 2). The completely independent young continued to call to their parents until day 18, but most of their time was spent resting and silent or ac-
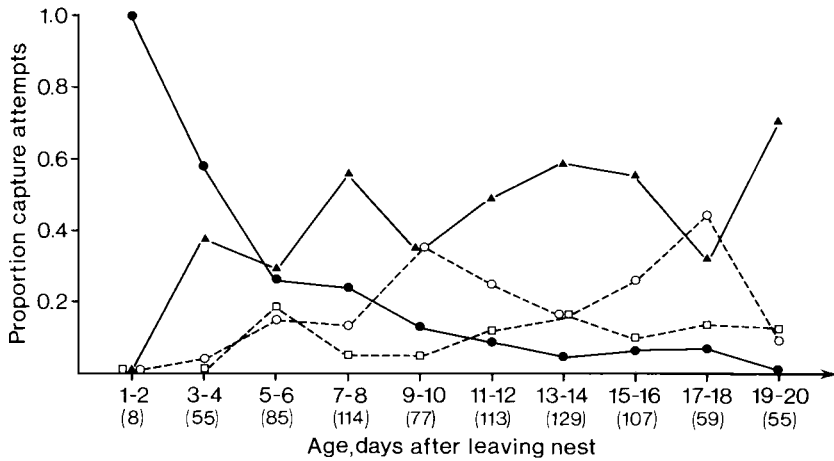
Fig. 3. Changes with age of the young in the proportion of foraging moves made as follows: Pecks at inedible objects (●), ground-gleaning (▲), perch-to-ground sallying (O), and aerial hawking (□). Numbers of capture attempts observed are given in parentheses on the age-axis. Data are presented for age intervals of 2 days.

tively foraging (Fig. 1). Throughout the period, the proportion of time that fledglings spent calling while resting decreased continuously ($r_s = -0.95$, 8 df, $P = 0.001$) while the proportions of time spent resting while silent ($r_s = 0.94$, $P < 0.001$) and foraging ($r_s = 0.66$, $P < 0.05$) continuously increased.

Young of the same brood often perched together on the same stone pile during the first week after leaving the nest and interacted only by pecking lightly at each other's feathers, bills, and toes. After the first week, chases between siblings became more frequent (Table 4), and this frequency increased up to the time of independence. Parents never showed any sign of aggression toward their own young but sometimes chased young of other broods from their territories.

The development of foraging techniques.—During the first 2 days after leaving the nest, the young were observed pecking at and manipulating only inedible objects like pieces of grass and moss, small stones, and flowers (Fig. 3). This behavior became less frequent with age ($r_s = -0.95$, 8 df, $P < 0.001$) (Fig. 3). On day 3, the young began to hop down from the stones where they were resting and made short and brief forays into the surrounding grass, where they pecked at different objects. These forays became more frequent after day 3, when the young were seen to make short bouts of hops on the ground, followed by a stop to scan the

surroundings (Fig. 3). This is one of the most frequently used feeding techniques of adult wheatears in short grass (Kneis and Lauch 1983, Moreno 1984), although adult birds usually run on the ground instead of moving by hops. It was the most frequently observed foraging technique throughout the study period (Fig. 3).

The young very often pecked when ground-gleaning, in the beginning usually once every stop (Fig. 4), but it was difficult to see whether or not they were directing their attacks at live prey. Up to day 9, both pecking rates and stopping rates increased in parallel; subsequently, stopping rates remained high while pecking rates started to decrease (Fig. 4). The young were more selective in their pecks at that stage and did not attack on every stop. After day 11, there was also a drop in stopping rates, the young making longer stops after each moving bout, and pecking rates decreased still further (Fig. 4). Pecking and stopping rates seemed to stabilize after day 12 (Fig. 4). The differences between these rates for the different 2-day intervals are statistically significant ($H = 20.8$, $P < 0.01$ for stopping rates; $H = 30.2$, $P < 0.001$ for pecking rates, 6 df). The young always selected areas with short grass or almost bare ground, like tracks and roads, for ground-gleaning.

Perch-to-ground-sallying and aerial hawking are common foraging techniques of adult wheatears (Moreno 1984). These probably require good prey-detection abilities and a pre-
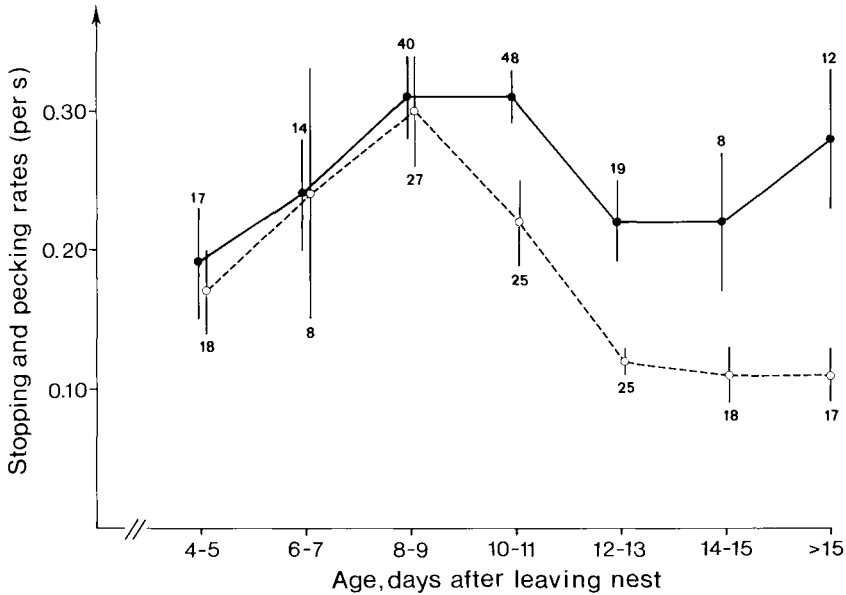
Fig. 4. Changes with age of the young in stopping rates (stops/s) (●) and pecking rates (pecks/s) (O) during ground-gleaning. Means and standard errors of rates grouped in 2-day intervals are shown. Numbers of timed observation runs for which rates have been calculated are given above (stops) or below (pecks) the standard errors.

cise attack. The young used them very seldom until day 5, and later the proportions of their use fluctuated widely (Fig. 3). Stand-catching, when the young remain stationary on a perch and attempt to catch prey as it flies past them (Davies 1976), was used mostly on days 5–9 (when it made up 4% of capture attempts) but was very seldom observed among older young.

The total attack rate of the young (attacks/min spent foraging), including all foraging techniques, increased with age ($r_s = 0.84$, 8 df, $P < 0.01$) (Fig. 5). The success rate, or proportion of attacks that ended with a prey being caught, generally increased throughout the period ($r_s = 0.60$, 8 df, $P < 0.05$, one-tailed), with two peaks, which are difficult to explain and could be due to variation between days in foraging conditions (Fig. 5). The observed success rates are probably underestimates, as the young may have captured items sometimes without my seeing them do so. The young usually swept their bills against some object after capturing prey, however, and this behavior was also used as evidence for capture success. Proportionally the most successful (25%) prey-capture technique was the seldom used stand-catching technique, which can be employed only when

prey fly past the perch at very short distances. Aerial hawking (13%) and ground-gleaning (12%) came next, whereas sallying was the least successful technique (7%).

The three usual foraging techniques were used differently ($\chi^2 = 17.7$, 6 df, $P < 0.01$) at different times during the morning as temperatures increased (Table 5). The young used the aerial hawking technique more frequently after 0900 in the morning than before, and they sallied more before 0800 than after (Table 5). Chasing the parents and trying to obtain food from them can also be considered a foraging technique. If we consider each chase as a capture attempt, and then compare the proportion of chasing with that of all other techniques during different hours, there was a drastic reduction in the proportion of chases after 0800 ($\chi^2 = 11.8$, 5 df, $P < 0.05$) (Table 5). I suggest that the young chased their parents more intensively early in the morning when they were hungriest and when the other foraging methods were less profitable because of low prey activity, as is shown by the low capture success rates between 0500 and 0700 (Table 5). With increasing temperature, foraging on their own became more rewarding, as is shown by their
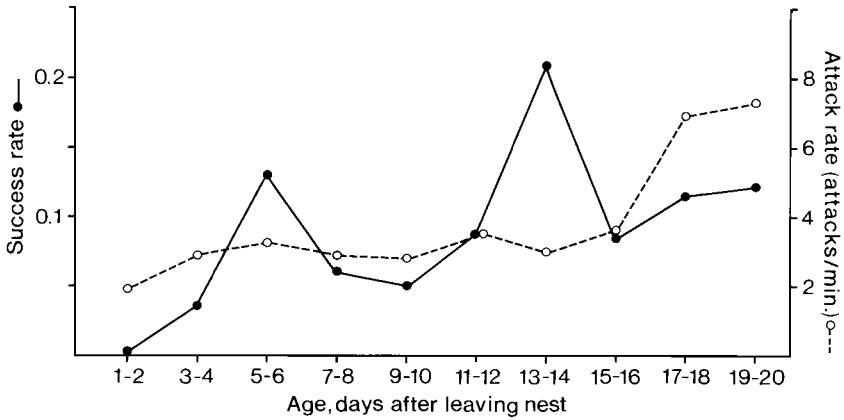
Fig. 5. Changes with age of young in attack rates (number of attacks/min observation time spent foraging) (right axis) and proportion of successful attacks observed (left axis). Data are presented for age intervals of 2 days. Minutes of observation time as in Fig. 1.

higher capture success between 0800 and 1000 (Table 5). After 1000 capture success decreased and chasing rates increased. Overall, there seemed to be a negative relationship between chasing intensity and capture success.

DISCUSSION

Labor and territory division.—There are few reports in the literature of the existence of a division of labor between parents in altricial birds after the young leave the nest (Hann 1937, Snow 1958, Grant and Grant 1980). The most detailed quantitative studies so far are those by Smith (1978) and Smith and Merkt (1980) on parental care of fledged young in the Song Sparrow (*Melospiza melodia*) and by Nolan (1978) in the Prairie Warbler (*Dendroica discolor*). Both Snow (1958) and Smith (1978) suggested that further studies of other species would indicate that a division of labor is a common phenomenon among altricial birds. Smith (1978) also

TABLE 5. Proportions of capture attempts by fledglings using different foraging techniques (values in parentheses are proportions of capture attempts when chasing parents is considered as another foraging technique), proportions of successful attacks, and mean temperatures for the six periods of the morning when observations were made. Number of capture attempts observed (*n*) is shown (in parentheses including chases).

Period	Ground-gleaning	Sallying	Aerial hawking	Other techniques	Chasing parents	Proportion successful attacks	Mean temperature (°C)
0500–0600 $n = 37$ (49)	0.38 (0.29)	0.46 (0.35)	0.05 (0.04)	0.11 (0.08)	(0.24)	0.027	9.9 ± 2.9
0600–0700 $n = 164$ (197)	0.61 (0.50)	0.22 (0.18)	0.12 (0.10)	0.05 (0.05)	(0.17)	0.085	9.7 ± 3.3
0700–0800 $n = 126$ (161)	0.53 (0.41)	0.32 (0.25)	0.08 (0.06)	0.07 (0.06)	(0.22)	0.135	12.4 ± 2.9
0800–0900 $n = 167$ (192)	0.69 (0.60)	0.20 (0.17)	0.08 (0.07)	0.03 (0.03)	(0.13)	0.156	14.5 ± 1.3
0900–1000 $n = 107$ (120)	0.51 (0.45)	0.20 (0.18)	0.23 (0.21)	0.06 (0.05)	(0.11)	0.159	17.0 ± 1.7
After 1000 $n = 49$ (64)	0.45 (0.35)	0.31 (0.23)	0.22 (0.17)	0.02 (0.02)	(0.23)	0.102	18.5 ± 2.7

offered several appealing hypotheses to explain its function. One of them was that the division of labor aids the parents in locating young and thereby reduces parental travel times and energy expenditure. If the young move and distribute themselves randomly in the territory, however, feeding only certain young may not help to reduce travel times between capture sites and feeding sites. To reduce the time spent by parents in moving to the different young, it would be advantageous if the young fed by one parent assembled within some restricted part of the territory and did not mix with those fed by the other. This would lead to a territory division between the mates, which could restrict their activity to certain parts of the territory where they could feed their respective family units.

The present data indicate that family division exists in the wheatear and suggest a division of the territory between the two family units during the time when the parents are feeding fledged young. Each parent tends to feed only certain young, which are not fed by the other, and the two groups of young are mostly fed on different sites by the parents. Young fed by the same parent are spatially aggregated in the territories, as they are on average nearer to each other than are young fed by different parents. Moreover, the young fed by one parent perch more often together than do young fed by different parents. Most young appeared to have favorite places where I could easily locate them. Although I did not collect quantitative data on spatial locations of parents except when they were feeding young, I observed them in the same parts of their territories that were used by their respective groups of young. Further studies should be concerned with a closer look at the distribution of foraging activities of the parents in the territories during this period. A division not only of feeding sites but of foraging areas could reduce travel costs between capture and feeding sites, and could allow better control of depletion and renewal of food resources and better knowledge of patch profitabilities (Kamil and van Riper 1982). The division of usual feeding sites between the parents became less marked during the second week, as compared with the first, because the mobility of the young increased, and chases after the parents became more frequent. The advantages of a clear-cut division of feeding sites diminishes with an increase in

chasing rates, as young do not have to be located while they are chasing, and as distances between capture and feeding sites are reduced. In sum, the present evidence suggests that a combination of ease in locating young and a consequent reduction in travel costs makes the division of labor adaptive in wheatears.

The second hypothesis of Smith (1978) seems to fit my observations less well. According to it, food delivery to each young is more easily regulated the fewer young each parent feeds. In the present case, young appeared to control their own feeding rates by begging during the first days and later by chasing the parents when hungry. The facts that labor division seemed to begin on day 4 for some pairs, which was the day when the young began to spread themselves out in the territory, and that there was some overlap in young fed by the parents at the beginning exclude the possibility that labor division is already established in the nest to facilitate the distribution of food between young. Reed (1981) also showed that there is no partitioning of the brood in the nest in Song Sparrows, and Smith and Merkt (1980) found complete division of labor only after day 5 in the same species.

It is probable that the initial movements of the young after fledging initiate the division of labor. The subsequent low mobility of the young during the first week probably makes the division of labor possible and profitable for the parents. It is not clear from my data, however, whether it is the young dispersing initially and being sought by the parents or the parents leading certain young to certain locations in the territory that initiates labor division. It may be an interactive process, in which certain young disperse to a site at which one parent is foraging that day. The parent begins to feed them there, the young get accustomed to being fed by that specific parent and call mostly to it, it stays in their vicinity and is attracted by their calls, and the process is reinforced until complete division of labor is achieved on days 3–8. Smith and Merkt (1980) have shown that the begging calls of Song Sparrow young are sufficiently individually specific to enable parents to recognize each young from a distance. If this is also the case with wheatears, it could aid parents in maintaining family units. The fact that the division of the brood between the parents is as equal as possible suggests that the young may also be

directly involved in its development. An equal division would be a consequence of an initial "ideal free distribution" (Fretwell 1972) of young between feeding parents. Nolan (1978) implied that there were stable family units over time in the Prairie Warblers he studied, and Smith and Merkt (1980) found few transfers of responsibility between parents for feeding specific young. In the present study, family units were clearly stable from day to day, and no transfer of responsibility was observed after full division of labor was achieved.

Interactions between parents and offspring.—Parental feeding rates of young seemed to increase slightly during the first days after the young left the nest and were higher than feeding rates of 14-day-old nestlings (Moreno in prep.). Smith (1978) found a similar pattern in Song Sparrows, and Royama (1966) suggested that the critical time of parental investment, which in its turn affects clutch size, is the first week after fledging date and not the nestling stage. Dependent fledglings probably have larger energetic expenditures because of an increased heat loss and costly activity like flight. A detailed study of the energy expenditure of the parents during the nestling and fledgling stages would be needed, however, to determine parental investment.

Young wheatears were dependent on their parents for 2 weeks after leaving the nest. This is shorter than for other passerines like the Spotted Flycatcher (*Muscicapa striata*) (18 days, Davies 1976), the Prairie Warbler (24–43 days, Nolan 1978), and the Song Sparrow (20–22 days, Smith and Merkt 1980). The time budgets of wheatear fledglings changed markedly during that time. They became more active and mobile, spent less time calling and waiting for the parents to feed them and followed them around more, and spent more time foraging. The pattern is very similar to that shown by young Spotted Flycatchers (Davies 1976), although these seem to spend a greater proportion of their time in foraging activities. Flight activity of fledgling wheatears seems to be intense only during days 7–10, which is the time when the young chase their parents most actively.

As in the Spotted Flycatcher (Davies 1976), it is during the second week that the young chase their parents most frequently while calling to them. This increase in chasing intensity coincides with a marked decrease in feeding rates by the parents and an increase in the pro-portion of feedings solicited by the young, that is, feedings preceded by a chase or by begging calls. Clearly the parents are forcing the young to feed themselves by becoming more reluctant to feed them. This is suggested by the fact that young were chasing their parents most intensively when the parents had reduced their feeding rates and were responding less to begging calls, as shown by the decrease in the proportion of successful chases. These data support the hypothesis of Davies (1978) that parental reluctance to feed the young forces them to become more and more independent. Even after 2 weeks, when the parents had ceased to feed them, the young continued to chase their parents and call to them. Further evidence of the effect of parental "meanness" is the marked increase in foraging activity after day 10, which coincides with a drastic drop of parental feeding rates to very low levels as well as a drop of the proportion of successful chases. At this point the young seemed to have no option other than increasing their foraging activity to substitute for dwindling parental food contributions.

Development of foraging techniques.—Young wheatears started to peck at a variety of objects and to manipulate them in their bills 1–2 days after leaving the nest. The same behavior has been observed in several other passerine species (Smith 1973, Davies 1976, Davies and Green 1976). It decreases as the young begin to catch their first prey and to react more readily to the stimuli emitted by them. Again, as reported for other species (Davies 1976, Davies and Green 1976), simple foraging techniques like ground-gleaning appear first, whereas those requiring more motor coordination and greater precision become important later on (sallying and aerial hawking). Young wheatears increased their attack rates in parallel with the proportion of time spent foraging, indicating their increasing reliance on feeding themselves. They also became more skilful foragers with age, as shown by their increasing success rates.

While ground-gleaning, young wheatears passed from an early stage, characterized by many short stops on the ground and many pecks, through an intermediate stage of many short stops but fewer pecks, to a final stage of fewer longer stops and even fewer pecks. Many of the pecks during the early stages were probably exploratory, although it was difficult to see at which objects the young directed their

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attacks. Later, they probably adjusted the duration of their stops to their detection capabilities and to the characteristics of the habitat. A diminution in the proportion of exploratory pecks might explain the trend in pecking rates.

The two other main techniques were less frequently used than ground-gleaning, probably because they were dependent on the flight performance of the young. Also, aerial hawking was used more frequently late in the morning, whereas sallying was more intensively used earlier in the morning. Before 0900, there were probably too few active aerial insects to make hawking profitable (Taylor 1963). Davies and Green (1976) documented a similar change in Reed Warblers (*Acrocephalus scirpaceus*). The sallying technique is directed toward terrestrial prey, which do not need to be so active to be detected from a perch. This technique can therefore be used early, when hawking is not possible.

Davies (1976) noted that young Spotted Flycatchers switched from begging food from their parents to feeding themselves when the last-mentioned strategy became more profitable in terms of energy intake. Young wheatears seemed also to switch between the two feeding strategies on a daily basis. They chased their parents intensively early in the morning when prey were inactive and capture rates low and switched to feeding themselves at about 0800 when rising temperatures led to an increase in insect activity and in capture-success rates. After 1000, capture success decreased again, probably because of higher probabilities of evasion from capture by fast-moving insects (Davies and Green 1976). Chasing increased then also, probably as a consequence of the lower success rates. There seems to be a clear relationship between the chasing intensity of the young and their capture-success rates. This suggests that young wheatears were able to choose the most profitable strategy according to foraging conditions.

ACKNOWLEDGMENTS

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