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Feeding-activity in some Insectivorous Birds

by JAN BOËTIUS.

(Med et dansk resumé: Fodringsaktivitet hos nogle insektædende fugle.)

The following observations have all been undertaken in Holte and the surrounding neighbourhood in the early summer of 1948.

Observations on the frequency of feeding have been carried out for a smaller number of species of birds, the number of feedings per 30 minutes has been taken as a unit. In addition, the length of time the birds stay in the nest during feeding has been measured with a stop-watch. Importance is attached to extending the observations over as large a part of the birds' working day as possible. In the instances referred to here rather reliable information is to hand regarding the age of the brood at the time of observation.

Many similar observations are to be found in ornithological literature, but, as they are usually taken under different circumstances — often without exact information as to the age of the brood and with other objects in view than the present — dificulties arise when comparing them with this material.

The Daily Effort.

It is of great importance to ascertain the age of the brood, as it is a well known fact that the intensity of feeding during the greater part of the time grows with the weight of the young. As an example is set forth here the increase in a brood of redstarts on three different observation days with uniform weather during the period of observation (4 hours daily observation at the *same* time of day).

Table 1. Redstart, *Phoenicurus phoenicurus*. (Clutch-size: **6**).

Date	Time of observation[1])	Age of clutch (days)	Average number of feedings per 30 min.
31-V.	8.00—12.00 (a. m.)	**6** (16)[2])	**8.5**
4-VI.	8.00—12.00 (a. m.)	**10** (16)	**10.0**
7-VI.	8.00—12.00 (a. m.)	**13** (16)	**11.3**

The material collected shows similar examples — in the following therefore only older broods with advanced feather development are compared — as a rule 3 to 4 days before flying, where the intensity of feeding is at a maximum.

Table 2.

Species	Date	Age of clutch (days)	Clutch-size	Time of observation (min.)	Av. nb. of feedings pr. 30 min.	Working day (hours)	Total numb. of feedings pr. day
Turdus merula	9-VI.	13 (15)	4	300	**(3.5)**		
Erithacus rubecula.....	24-V.	12 (14)	6	1050	**7.5**	18	**271**
Phoenicurus phoenicurus	7-VI.	13 (16)	6	480	**10.1**	15.5	**313**
Ficedula hypoleuca	18-VI.	7 (?)	6	330	**(10.7)**		
Sturnus vulgaris	26-V.	18 (21)	7	720	**10.0**	15	**300**
Parus palustris.....	26-V.	13 (18)	7	720	**7.3**	16	**237**
Parus caeruleus.....	2-VI.	14 (18)	9	990	**30.3**	16.5	**1000**

The frequency of feeding appears from table 2 to be about 7-10 per 30 min. for the species investigated. The entries for *Turdus* (which has a low frequency) and *Ficedula* are put in brackets, as the observation period in both cases was very short — moreover as far as *Ficedula* are concerned, a rather infant brood (7 days) is under consideration — unfortunately the observations came to a tragic end, as a cat ate all six young.

On the other hand the Blue Tit stands apart from the rest in that it has an extremely high activity and it is specially remarkable that the two *Parus* species differ so much in this respect.

In the next to last column of table 2 the approximate length of the working day is shown. The Robin has the longest active

[1]) All times are given in mid-European time (Danish summertime÷60 min.).

[2]) The figures in brackets after age give the total number of days which the young spend in the nest.

period (app. 3.00 a. m.—10 p. m.) while the other species work for about 16 hours out of 24. The Starling and *Parus* species

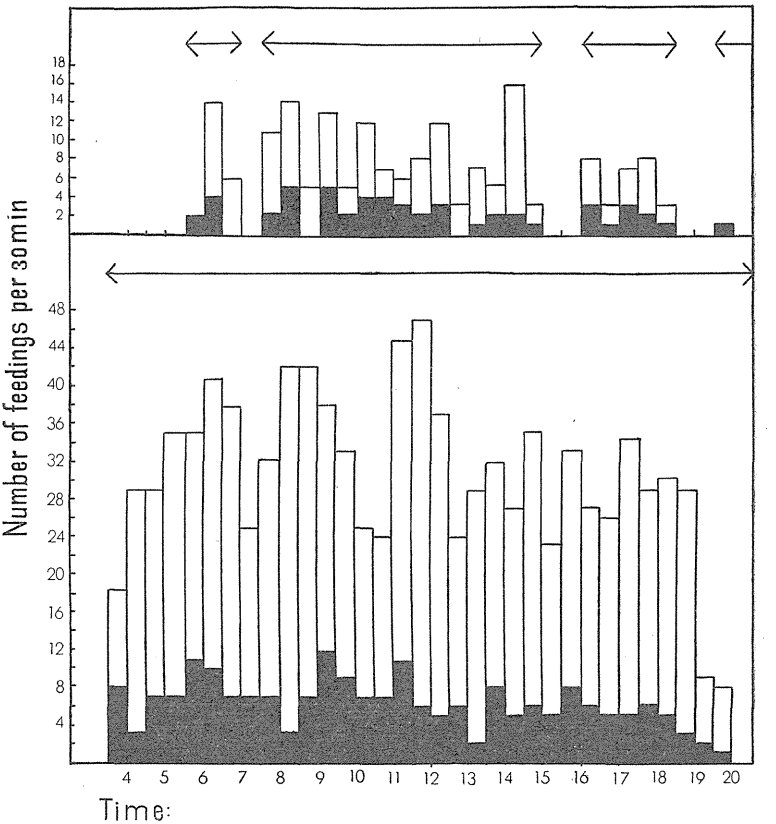

Fig. 1. Intensity of feeding. Marsh-Tit, *Parus palustris* (the above diagram). 26-V-1948. Age: 13 days. Clutch-size: 7. — Blue Tit, *Parus caeruleus* (the diagram below). 2-VI-1948. Age: 14 days. Clutch-size: 9.

Horizontal axis: Working day divided in 30 min.-units.

Vertical axis: Number of feedings pr. 30 min. and number of excrements carried out pr. 30 min. (black columns).

The horizontal arrows indicate the period of observation.

Fodringshyppighed hos Gråmejse (øverste diagram) og Blåmejse (nederste diagram). Abscisse: *Fodringsperioden opdelt i enheder på 30 min.* Ordinat: *Antal fodringer pr. 30 min. og antal ekskrementer udbåret pr. 30 min. (de sorte søjler). De vandrette pile angiver observationsperioden.*

begin the day at about 3.30 a. m. and cease at about 7 p. m. (starling) and about 8 p. m. (tits). The Redstart does not begin untill 5 a. m., but on the other hand continues longer into the evening (until about 9 p. m.). In the last column is to be found an approximate figure, calculated according to the length of the working day, for the total number of feedings per day. The number of feedings are between 2 to 300, still with the exception of the Blue Tit, which reaches 1000 feedings per day. Since I have controlled the whole feeding period during these 24 hours, all the 1000 feedings are directly observed. Strangely enough, BORNEBUSCH arrives at exactly the same figure for the Blue Tit, according to a calculation during an extremely short period of observation. The frequency of feeding can therefore vary considerably in the different species, also as far as such closely related kinds as the Blue Tit and Marsh-Tit are concerned. Let us return to this example and consider fig. 1, which shows the progress of feeding for these two species for the two days recorded in table 2.

The Blue Tits' visits to the nest take place with unabated energy the whole day — the relatively infrequent visits of the Marsh-Tit are of a far more fluctuating nature. Where lies this difference? There is no doubt that two broods of young of the same age, belonging to two so closely related species, need about the same supply of food.

The fact that in this case the Blue Tit has two more young in the brood than the Marsh-Tit cannot possibly explain why its frequency of feeding is app. four times as large as the latter's.[1]) This remarkable difference lies to a great extent in

The Nature of the Food.

The Marsh-Tit feeds its young with small green caterpillars which it collects in its beak often a dozen at a time. The difficulty in getting food connected with the various times of the day is undoubtedly contributory to the very inconstant intensity of feeding, although hardly the only reason — more about this later.

[1]) A paper by MOREAU (1947) referring to tropical species clearly indicates that intensity of feeding increases in correspondence with an increase in clutch-size, but not in proportion hereto.

The Blue Tit, on the other hand, feeds almost entirely on "invisible" insects and larvae, which it apparently can find everywhere, often in the tree where the nest is built; in the least it does not appear to have any periodical difficulties in getting hold of these small insects. On those occasions (app. 15 in all) when I have been able to follow the Blue Tit's flight after food from the time it leaves the nest to its return, I have seen it snatch "invisible" insects from 4 to 13 times per trip. It has not been possible for me to determine these insects, but they are so small that one can rarely see them in the bird's beak, even when using strong binoculars. It is curious that on only one occasion during the 1000 feedings observed, did the food differ from the kind mentioned, when the Blue Tit took home a big green larvae, at least 2" long.

It is interesting to note that during those periods when the Marsh-Tit itself forages between feedings, it eats insects of the same size which the Blue Tit uses for feeding. I had ample opportunity to ascertain this when the Marsh-Tit parents foraged in the apple tree where their box was hung up.

It is obvious that the birds adjust the sort of food according to the size of the young ones, but at the late stage of breeding recorded, the species investigated quite definitely had certain specialities as predominant feeding stuffs. The Blackbird fed almost exclusively with earth-worms of medium size, brought home in considerable quantities, which were very carefully divided between the young ones, corresponding well with the low frequency of feeding. The Robin specialised to a great extent in fat, dull green larvae, about ½" long (perhaps Syrphides). The male Redstart used almost exclusively big light green caterpillars, while the female redstart mainly took reddish-brown larvae of the same order of insects. The Starling fed almost entirely with Tipulide grubs and earth-worms.

Change in the intensity of Feeding.

The purpose of this examination has been to ascertain whether the feeding was done at a regular speed all day long, or whether a certain rhythm could be established. Observation of the Blue Tit and Marsh-Tit proved that the speed varies considerably for the various species.

FRANZ (1937) has found in *Dryobates leucotos* that a curve, showing feeding of 7 day old birds, will clearly show two maxima. PALMGREN (1938) states that this, and similar examples from other species, might be taken as two common phases of the day's activity for the birds in question. Investigations of the comparative singing intensity during the day confirm this supposition (PALMGREN 1932).

While neither the Marsh-Tit nor the Blue Tit seem to show anything like two phases, there might be grounds for this sup-

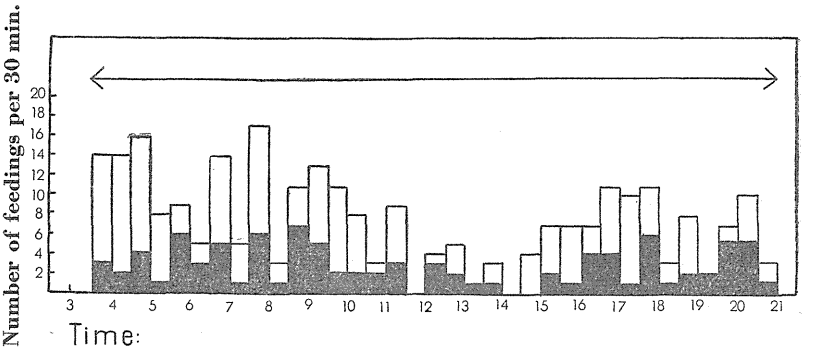

Fig. 2. Intensity of feeding. Robin, *Erithacus rubecula*. 24-V-1948. Age: 12 days. Clutch-size: 6. Signature as in fig. 1.

Fodringshyppighed hos Rødhals. 24-V-1948. Kuldets alder: 12 dage. Kuldets størrelse: 6. Signatur som fig. 1.

position for the Robin. The above mentioned conclusions of PALMGREN are as a matter of fact occasioned by a study of the restlessness of the Robin during the periods of passage, and in this connection a clear two-phased day activity in the periods of experiment outside the real time of passage was proved.

Attention should also be payed to a paper by LEES (1948). The author has carried out trapping experiments in order to determinate the feeding hours of adult birds during the winter. Here once more the Robin shows two well separated maxima of activity, the first in the hours after sunrise and the second in the hours before sunset.

Fig. 2 shows that the Robin's working hours are more or less divided into two periods of greater activity, separated by a noticeably passive period 11.30 a. m.—3.00 p. m.). In the

first active period of the day the intensity on an average is higher than during the second, but especially early in the day the feeding is characterised by shorter active and longer passive periods.

Fig. 3 shows the Starling's feeding activity during the day, and neither can two phases be found here. The Starling is, like the Blue Tit, an example of a bird which feeds at a regular speed during the whole day, and even for the short periods which are chosen here, there is not, as with the Robin, to be

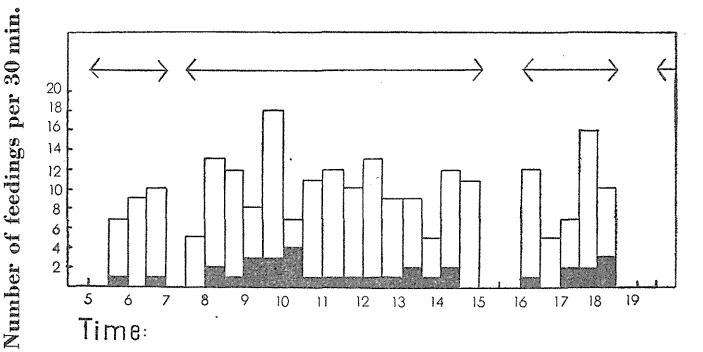

Fig. 3. Intensity of feeding. Starling, *Sturnus vulgaris*. 26-V-1948. Age: 18 days. Clutch-size: 7. Signature as in fig. 1.

Fodringshyppighed hos Stær. 26-V-1948. Kuldets alder: 18 dage. Kuldets størrelse: 7. Signatur som fig. 1.

found any change between shorter active and longer passive periods.

There is also the possibility of two-phased activity with the Redstart, as with the robin, but the best observation day only extends to 8 hours (or about 50 % of the whole feeding time), so the changes cannot be observed sufficiently clearly.

Table 3 shows the difference between the effort before and after 12 o'clock in percentage of the total number of feedings observed (3rd and 6th column). With the exception of the Robin, which shows a considerably lower activity during the last half of the day, as a rule the work is almost regularly divided between the two halves of the day. But it is characteristic that the effort is regularly slightly greater before 12 o'clock than after that time, which may be taken as a result of tiredness.

Table 3.

Species	a. m. observations			p. m. observations		
	Time of obs. (hours)	Nb. of feedings	% of total nb. of feedings obs.	Time of obs. (hours)	Nb. of feedings	% of total nb. of feedings obs.
Erithacus.....	8,5	160	62	8,5	100	38
Phoenicurus ...	4	90	(54)	4	77	(46)
Sturnus	6	122	53	6	109	47
Parus palustris	6	98	56	6	78	44
Parus caeruleus	8	511	52	8	471	48

The robin's two-phased feeding curve may be "explained" by the fact that this bird is suited for weaker light than the other species mentioned here, and therefore had longer working hours, possibly compelling a rest in the middle of the day.

Method of Action of the Feeding Instinct.

Fig. 4 gives a characteristic selection of the feeding observations collected, arranged here in a clearer way than in the summarised diagrams. The question is whether a certain rhythm of feeding can be shown.

As regards the Robin, it can be seen how the feedings at certain times form points of compression (marked on fig. 4 with x), which are separate from more passive periods. There seems to be a certain regularity (app. 1 hour's interval) apparently caused by the fact that the feeding instinct works especially strongly in these intervals. It was ascertained during the observations that during these especially active periods the food was captured nearer to the nest than otherwise, and the matter can also be explained by the fact that for various reasons the birds have been forced to alter hunting grounds rather regularly. On the short trips, however, the Robin returned home with considerably smaller and fewer articles of food than usual, and it appears likely to me that here one can see an indication that the birds are forced to find an outlet for their feeding instinct, which at this time works especially strongly, by the augmentation of the number of feedings per unit of time. From the longer trips taken during the more passive periods,

to a hunting place in a glade about 200 yards from the nest, the food brought home was almost entirely the Syrphide larvae previously mentioned, while in the interval of short activity, apparently more arbitrarily chosen insects were brought home.

This division of activity is not nearly so clear in the Starling, or, to use the above-mentioned interpretion, it does

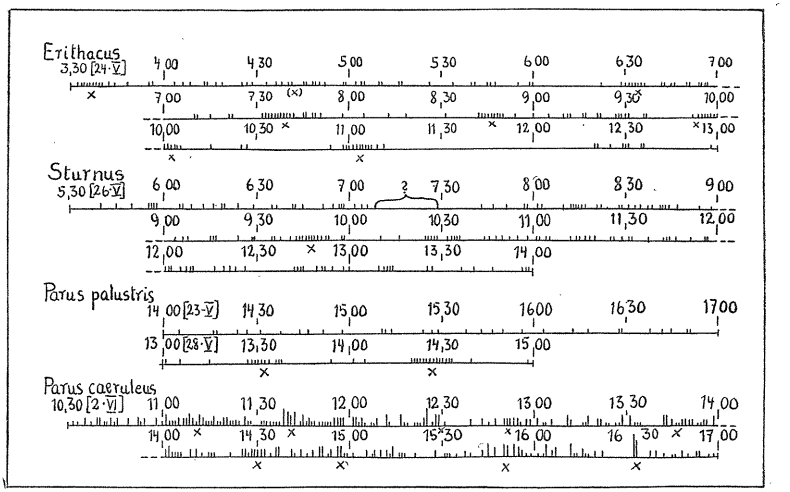

Fig. 4. Points of time for feeding arranged on a time-axis (unit: 1 min.). In the case of *Parus caeruleus* the lengths of the vertical marks indicate the number of feedings for the minute in question.

Fodringstidspunkter ordnet på en tidsakse (enhed: 1 min.). Hos Blåmejsen (Parus caeruleus) *antyder længden af de lodrette mærker antallet af fodringer i det pågældende minut.*

not seem to possess a feeding instinct which works so distinctly periodically as that of the Robin. The hunting ground of the starling was a nearby field, and with each feeding it could be seen already from app. 50 yards distant, flying in exactly the same direction to the nest, just as the composition of the food the whole day through varied very little.

For long periods the Marsh-Tit could feed very evenly (fig. 4, first horizontal line), and at other times showed decided compression (fig. 4 second horizontal line). In the instance depicted of the last-named kind, where one can see two strongly active, shorter periods, following intervals of passivity, the passive period was used by the parents for foraging for themselves,

which took place in the tree where the nest was built. The two active periods seem to show that the feeding instinct had been saved up, causing especially active feeding. It is doubtful whether true compensation is brought about by this method, as it is hardly likely that in these active periods the young ones receive more food per unit of time than usual.

The feeding instinct of the Blue Tit seems to work strongly and evenly during the whole of its working day. It is rather doubtful whether the short, specially active periods marked in fig. 4 show any tendency for periodicity.

A similar phenomenon to that just referred to in regard to the Marsh-Tit was also observed in the Blue Tit. The feeding bird stayed in the nest from 4.22 p. m.—4.32 p. m., the longest stay recorded during the entire day of observation. When it again left the nest, it showed an absolutely amazing activity, so that in the following two minutes it fed 8 and 5 times respectively, and it was quite certain that it was the same bird which fed. As described earlier, I have a number of times followed the whole of the Blue Tit's hunting trip and ascertained that on each trip it collected 4 to 13 "invisible" insects. In the strongly active 2-minute period just referred to with 13 feedings in all, the bird took 1 to 2 "invisible" insects on each of the very shortest hunting trips, which all took place within an area very near to the tree where the nest was placed. This gave the observer a strong impression that as far as the bird was concerned it was a matter of satisfying much accumulated feeding instinct by carrying out as many feedings as possible in a short time.

To put it briefly, in the Robin it appears to be a matter of a periodically working feeding instinct, which spreads itself over the most of its long working day, whereas the instinct of the Starling and the two species of Tits investigated work more evenly when there are not, as in the examples given for the tits, any special circumstances which may cause an accumulation of the instinct, which can result in a subsequent shorter period of great activity.

The Male's and Female's Mutual Participation in the Feeding.

With the exception of the Blue Tit, it was definitely ascertained that both parents among the birds investigated took part in the feeding.

With the Blackbird the work was equally divided between both parents, in the Robin this was almost also the case. Here there was a clear difference between the two birds, but their sex could not be established. According to LACK (1947) one certain difference in sex which can be established in the field is that the male feeds the female. Unfortunately I received this information after the young ones were almost grown up, and it was too late to use it. Both birds, however, participated during the entire observation period. The feedings were often double feedings, that is to say the birds fed immediately after each other when they returned at the same time from a hunting trip, as was sometimes the case. If they did not arrive simultaneously, it could happen that the one awaited the arrival of the other before feeding took place. This was possibly caused by shyness against the observer. The nest was in the middle of a wood, and the birds were quite unused to people at close proximity.

As to the Redstart, both birds are active, but in a rather changeable mutual manner. Table 4 shows the parents' activity regarding feeding and removal of excrement during three different days.

Table 4. Redstart, *Phoenicurus phoenicurus*. (Clutch-size 6).

Date:	Number of feedings						Number of excrements carried out					
	31-V.		4-VI.		7-VI.		31-V.		4-VI.		7-VI.	
	male	fem.	male	fem.	male	fem.	male	fem.	male	fem.	male	fem.
Time of obs. (a. m.)												
8,00—8,30	5	5	6	4	2	1	3	1	1	1	0	1
8,30—9,00	4	3	5	6	10	6	1	1	2	3	2	3
9,00—9,30	8	5	3	5	7	9	2	2	1	2	2	5
9,30—10,00	6	3	5	8	2	9	1	0	2	4	1	5
10,00—10,30	2	3	3	8	1	4	1	2	1	1	0	1
10,30—11,00	5	5	4	7	3	6	1	1	1	2	0	3
11,00—11,30	5	5	3	7	8	7	4	1	1	1	2	1
11,30—12,00	2	5	1	5	5	10	0	3	0	1	2	4
Total:	37	31	30	50	38	52	13	11	9	15	9	22

According to the table the female does the most work, as she carries out 133 of the 238 feedings observed (or 56 %) and removes 48 of 69 excrements (or 70 %).

In the Pied Fly-Catcher the woork during the short period of observation was equally divided between the sexes. The same seems to be the case with the Starling and the Marsh-Tit; at any rate during all the 30 min. periods of observation, both birds could be seen feeding.

As far as the Blue Tit was concerned, strangely enough not once during the day of observation were both parents to be seen at the same time, and as it was impossible to discern any individual distinctive marks, it could not be established whether one or two birds were working. There is, however, reason to believe that both birds participated, as such a performance would be quite unbelievable if only one sex took part. On the assumption that both parents joined in, the immence precision with which the birds adjust the extremely short feeding intervals after each other is rather peculiar.

It was observed several times in the Redstart, Pied Fly-Catcher, Starling and Marsh-Tit (the Redstart lived in a shed, the others in boxes), that the male fed via the female when she was in the nest on his arrival.

Disposal of Excrement.

Both parents of all the species investigated, in close connection with feeding, fly away with excrement, which presumably is thrown on the ground a little distance from the nest. In the Robin I noticed once or twice that it carried an excrement to a particularly visible place in a spruce only about 10 yards from the nest. There does not seem to be any simple

Table 5.

Species	Number of excrements per hour per young	Number of excrements carried out per feeding
Turdus	0,75	0,43
Erithacus	0,90	0,35
Phoenicurus	1,29	0,34
Ficedula	1,00	0,28
Sturnus	0,29	0,14
Parus palustris	0,63	0,30
Parus caeruleus	1,29	0.21

rule for changes in evacuation activity with increasing age. In table 5, therefore, only observations from those days covered by table 2 are given.

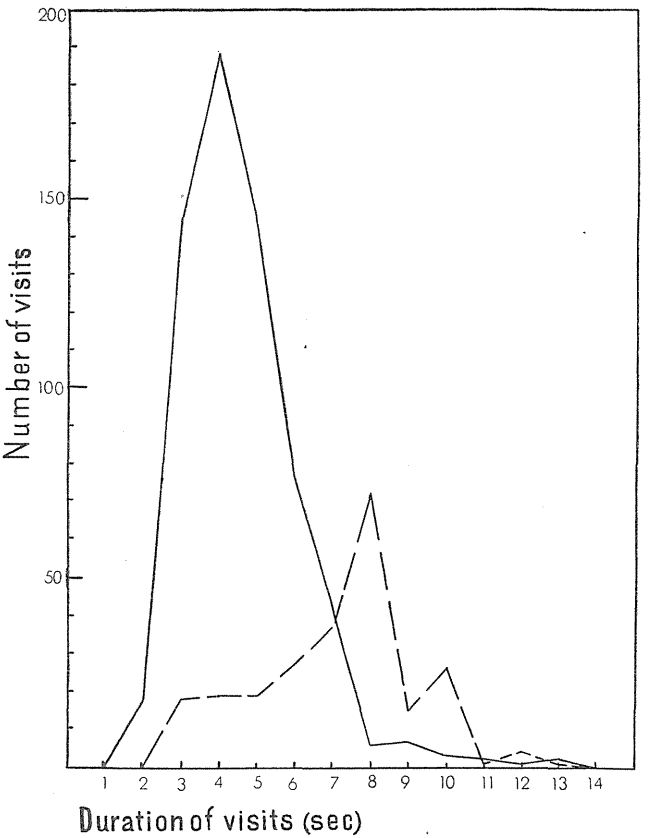

Fig. 5. *Parus caeruleus.* Curves showing the duration (seconds) of nest-visits during a usual feeding (——) and during visits in connection with the removal of excrements (- - -).

Blåmejse. Fordelingskurver visende varigheden (i sekunder) af redebesøg ved almindelig fodring (——) *og af besøg, hvor tillige ekskrementer blev udbåret* (- - -).

From Column 1 it can be seen that activity is greatest in the Redstart and Blue Tit, while the young Starlings excrete far more seldom. Strangely enough, also in this respect there is a considerable difference between the Blue Tit and Marsh-Tit, but this may perhaps be caused by unreliable statistics, as

the Marsh-Tit was the only one of the birds observed which was seen to eat the young ones' excrement during its stay in the nest.

From the second column it can be seen that while in the case of the Blackbird, which showed a very low frequency of feeding, the excrement was removed with apparently every alternate feeding, in the Blue Tit this happens about every fifth visit to the nest.

The excrement is removed immediately after each evacuation, which is very likely released by the feeding bird's arrival at the nest. Fig. 5 shows a diagram for the Blue Tit with two feeding curves, respectively for the duration of ordinary visits to the nest, and those which are connected with the carrying away of excrement. It appears that an ordinary feeding usually lasts about 4 seconds, while feeding + waiting time + carrying away of excrement lasts about 8 seconds, that is to say that evacuation itself lasts about 4 seconds. In the Robin, where the process only lasted about 3 seconds, I could observe how the bird, which fed in a half-open nest, quietly awaited the appearance of the excrement.

DANSK RESUMÉ

Fodringsaktivitet hos nogle insektædende fugle.

Der er foretaget observationer navnlig af Rødhals, Rødstjert, Stær, Gråmejse og Blåmejse. Da fodringshyppigheden (i figg. 1-3 udtrykt i antal fodringer pr. 30 min.) stiger med ungernes alder (se tabel 1), bruges til sammenligning af arterne data fra iagttagelselsesdage, der ligger 3-4 dage før kuldets udflyvning. I tabel 2 (sidste kolonne) er fremstillet de undersøgte arters beregnede antal fodringer pr. dag.

Blåmejsens aktivitet er betydelig større end de øvrige arters og særlig påfaldende er den i modsætning til den nærstående art, Gråmejsen (se fig. 1). Der vises, at dette forhold bl. a. skyldes forskelligheder i foderets art.

Det vises endvidere, at alle de undersøgte arter er mest aktive i dagens første halvdel (se tabel 3). Rødhalsen har i modsætning til Stæren og Mejserne en udpræget totoppet fodringskurve dagen igennem, og den har tillige den længste ar-

bejdsdåg (fig. 2). Stæren fodrer med ret jævn hastighed dagen igennem (se fig. 3).

Der vises (bl. a. på fig. 4), at Rødhalsens fodring sker under afvekslende korte aktive perioder og længere mere passive perioder, hvad der ikke gælder med så stor tydelighed for de øvrige arter. Det formodes, at der hos Rødhalsen er tale om en periodisk virkende fodringsdrift. Hos de to mejsearter omtales, at de under særlige omstændigheder (f. eks. efter forudgående fouragering) i kortere perioder kan udvise usædvanlig høj fodringsaktivitet, og det synes som om fodringsdriften i den nærmest forudgående tid er blevet "akkumuleret".

Hos alle de undersøgte arter deltager han og hun omtrent ligeligt i fodringsarbejdet; dette er dog ikke med sikkerhed påvist for Blåmejsen. Tabel 4 viser arbejdsfordelingen mellem han og hun m. h. t. fodring og ekskrementudbæring hos Rødstjerten. Tabel 5 (1. kolonne) viser antal af ekskrementer afgivet pr. time pr. unge og kolonne 2 viser antallet af ekskrementer afgivet pr. fodring. Endelig vises på fig. 5 hvorledes opholdstiden i reden for et sædvanligt fodringsbesøg (den fuldt optrukne fordelingskurve) hos Blåmejsen ligger i forhold til tiden for fodring, når samtidig et ekskrement afgives (den stiplede kurve). Det ses, at ekskrementafgivningen, der sikkert sættes reflektorisk i gang, når den fodrende fugl ankommer til reden, varer ca. 4 sekunder.

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