Parental care of nestlings by the Goldcrest *Regulus regulus*

SVEIN HAFTORN

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The sharing of parental duties is described, with emphasis on the feeding aspects. Both sexes feed the young, but the contribution of each parent depends on the time relationship between overlapping double broods. The waiting time before excrement removal after meals is adjusted to the age of the nestlings. Large-sized young are able to 'shoot' their excrement outside the nest cup, independently of parental presence. Only the female broods the nestlings. When brooding, she makes 'tremble-thrust' movements, one function of which may be to enlarge the nest cup, thus providing the numerous nestlings with more space as they grow. It is argued that the parental investment of the Goldcrest is considerable and that the full cooperation of both parents throughout the reproduction period is necessary for success in rearing two broods a year.

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Introduction

In the Goldcrest *Regulus regulus* some nest duties are shared, while others are restricted to one sex or the other. For example, both parents take part in nest building and in feeding the young, but only the female is concerned with incubating the eggs and brooding the young. In Fennoscandia, as in Central Europe, the Goldcrest regularly rears two broods, which overlap in time (Palmgren 1932, 1959, Haftorn 1978a, Thaler 1979).

In the present paper I describe the parental behaviour and intersexual cooperation during the nestling period, and attempt to show that the proportion of the joint parental duties carried out by each at any one time is modified to fit the prevailing circumstances and to facilitate the rearing of double broods.

Material and methods

This paper is mainly based on the data from three different nests at Målsjöen in Klaebu, about 25 km S of Trondheim in Norway. The two nests studied in 1971 contained the first and second broods of a single pair (nest 1/71 and 2/71), while that studied in 1974 held the first brood of a different pair (nest 1/74). All nests were observed by means of closed-circuit TV. The male and female of the first pair could be told apart by slight differences in their head patterns, those of the second pair because the female had been ringed.

Hatching

As the female starts her effective incubation during the egg-laying period, the eggs usually hatch over a period of 2—3 days (Haftorn 1978a, Thaler 1979). As a rule, the egg-shells are removed by the female, seldom by the male, though this was once observed to happen when the female was

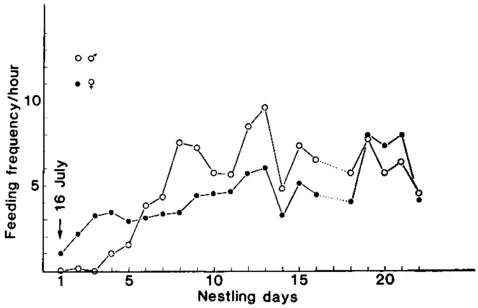

FIG. 1. The mean hourly feeding frequencies recorded daily for a second brood of 5 young (nest 2/71).

absent. In contrast to Thaler's (1979) experiences, the female has also been seen to eat pieces of egg-shell lying in the nest, before removing the remainder.

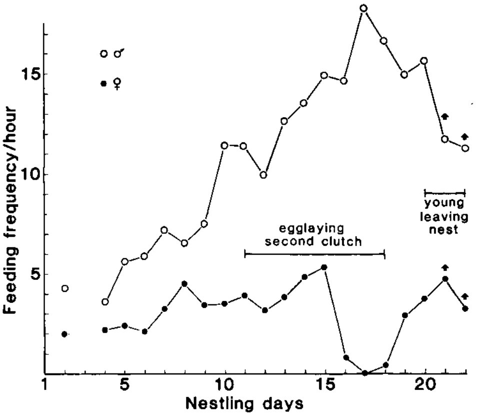

FIG. 2. The mean hourly feeding frequencies recorded daily for a first brood of 7 young (nest 1/71). Arrows indicate that the values shown represent only the minimum number of possible feeding visits, because some fledglings were situated outside the observation range of the television camera. The egg-laying period for the pair's second clutch (nest 2/71) is also shown (for details see text).

Brooding

As with incubation, only the female is concerned in brooding the young. The newly-hatched young, which are quite naked except for small patches of down on their heads, need about the same degree of attention as the eggs, but from the 6—8th nestling days onwards, the female's attentive time decreases rapidly, and after the 10—13th days the female does not normally brood any more during the daytime (Haftorn 1978a). By the latter stage the nestlings' back feathers have broken through their sheaths and, although far from being fully developed, the plumage now evidently provides sufficient insulation to prevent the young from cooling down when lying together within the feather-lined nest. According to Thaler (1979), a nestling on its own is unable to keep its body temperature at a steady level (41°C) until it is 18—19 days old.

Soon after the female has ceased to brood the young during the daytime, she also leaves them alone during the night. My observations of night-time brooding are only sporadic, but at one nest the female stopped the daytime brooding on Day 10 and as from the next day she was also absent during the night. According to Thaler (1979) the female does not spend the night in the nest after the young are 8 days old.

Feeding the young

Feeding frequency during the nestling period. On an hourly basis, feeding frequency increased semi-linearly from about 0.5—4.0 visits on the first nestling day¹) to a maximum frequency of about 15—24 visits during the latter

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¹) Equivalent to the start of hatching.

part of the nestling period. For the two broods of 5 and 7 young, respectively, maximum feeding frequency was attained on Days 13 and 15, after which the frequency levelled off (Figs. 1—2). For the brood of 10 young feeding frequently tended to increase throughout the nestling period (Fig. 3).

As would be expected, feeding frequency was related to brood size (Fig. 4). However, when the data are expressed as the number of feeds per nestling per unit of time, the feeding rate did not increase proportionally with brood size (Haftorn 1978c).

During the first 5 nestling days, for the nests studied, the mean number of feeding visits per nestling per hour varied from 0.6 to 1.5, increasing to 1.5—3.2 during the latter half of the nestling period (Fig. 5). It should be pointed out that 'number of feeding visits' is not equivalent to the actual 'number of meals' received by each nestling, because the parents usually bring back several food items on every occasion and may share these out between two or more nestlings.

Feeding frequency throughout the day. At nest 1/74, with 10 young, continuous observations were made on Day 4 (3 June), from 03.50 to 20.30 hrs (1000 minutes) and on Day 8 (7 June) from 03.00 to 20.42 (1062 minutes). On the former date a total of 125 feeding visits were recorded, on the latter date 213. During the course of both days these feeding visits were fairly evenly distributed, with the exception of a distinct evening peak on Day 8 (Fig. 6).

Duration of feeding visits and nest sanitation. The feeding visits made to a nest normally last longer than the actual time needed for giving the food to the young, because the parents wait a while afterwards in case the young defecate. The faeces of small nestlings, up to 2—3 days old, are eaten

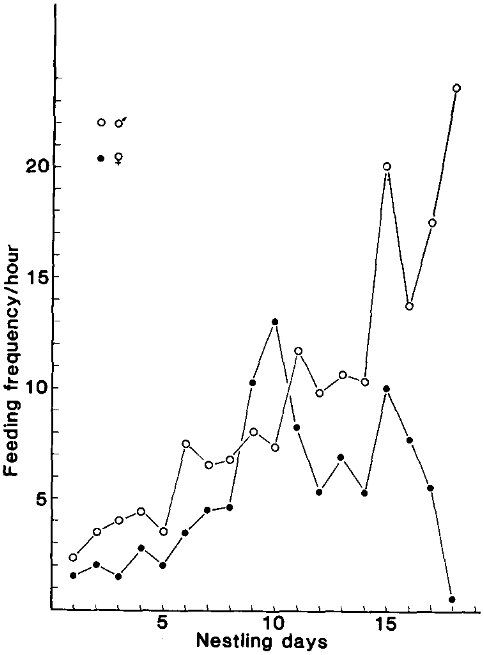

FIG. 3. The mean hourly feeding frequencies recorded daily for a first brood of 10 young (nest 1/74).

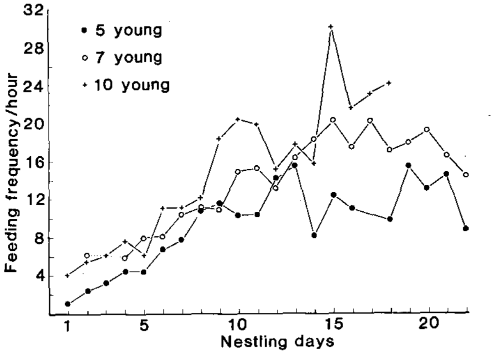

FIG. 4. The hourly feeding frequency values for both sexes combined for the three nests shown in Figs. 1—3, containing 5, 7, and 10 young, respectively.

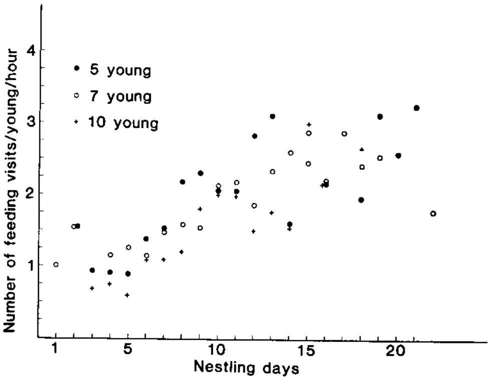

FIG. 5. The mean hourly feeding frequencies per nestling per day, based on the combined data for the three different nests (1/71, 2/71, 1/74).

immediately by the parents (Thaler 1979, and own observations). Thereafter they are removed by the parents.

As is typical of passerines, it takes considerably longer to feed newly-hatched young than older ones, and the waiting time for possible excrement production is also much longer for young than for older nestlings. Both parents devote about the same amount of time to these activities (Fig. 7). On average, the male and female parents of the double brood 1—2/71 spent 15.1 secs ($N=13$) and 22.5 secs ($N=17$), respectively, on feeding young nestlings (0—5 days old), compared with only 4.3 secs ($N=36$) and 3.1 secs ($N=44$), respectively, on feeding nestlings more than 5 days old. Furthermore, the waiting times for possible excrements were 16.0 secs ($N=14$) and 15.4 secs ($N=19$), respectively, for the young nestlings, compared with only 8.8 secs ($N=46$) and 10.1 secs ($N=43$) for those more than 5 days old. Whether or not the young in fact defecated, the duration of the waiting times was the same (male: mean waiting times, with and without defecation, respectively, were for young nestlings 18.1 and 16.5 secs, for older nestlings 9.1 and 9.3 secs; female: 18.5 and 16.3 secs for young and 7.9 and 10.6 secs for older nestlings).

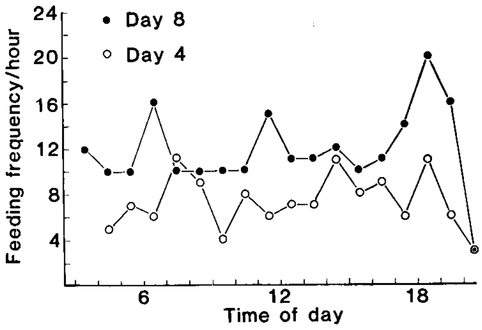

FIG. 6. The mean hourly feeding frequencies recorded throughout the 4th and 8th nestling days at nest 1/74, containing 10 young.

As is seen in Fig. 7, the feeding times for young nestlings varied greatly. Whereas almost all the older nestlings (i.e. more than 5 days old) swallowed their food within 5 secs after the arrival of the parent, the feeding times for young nestlings ranged from 2 to 110 secs. The reason for this marked difference is evident. Young nestlings, especially the newly-hatched ones, do not respond as quickly when offered food as the older nestlings do, and the parent bird must often patiently stand and repeatedly proffer food before the nestling(s) finally raises its head and gapes. Moreover, if a nestling does not swallow the food properly, i.e. the food item(s) remains in its mouth or throat, the parent carefully removes the food and starts the feeding process all over again. Sometimes it may even give up and proffer the food to another nestling.

If the young defecate in the absence of the parents — it sometimes happens

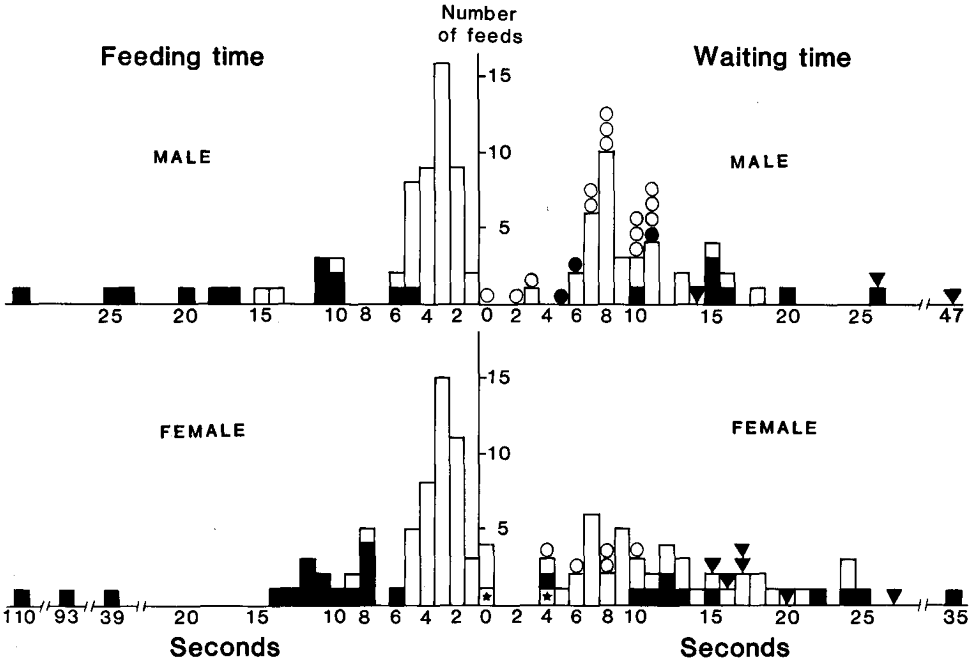

FIG. 7. The time taken to feed the nestlings and the subsequent time spent waiting for defecation. Values for the male and female parents shown separately. Black symbols and histograms denote nestlings less than 6 days old, white symbols and histograms those 6 days old or older. Circles indicate that the waiting-time was 'rewarded' by a dropping, which was then removed by one of the parents. Triangles indicate that the excrement was eaten by one of the parents and stars that egg shells were removed.

that the waiting times of the parents are cut too short — then the faeces are normally removed on the occasion of the next visit to the nest.

When the nestlings have reached an age of about 13 days, they start 'shooting' their faeces outside the nest cup. They may do this by elevating their rump while still sitting inside the nest cup, but very often they move backwards out of the nest and defecate sitting on the nest rim, or clinging to the outside of the nest (Fig. 8), whereafter they immediately creep back inside the nest again. The faeces then either fall down outside the nest, or stick to the outer nest wall. In the latter case the faeces are usually removed by the parents later on. This habit of independent defecation develops towards the end of the nestling period, at the same time as the parents become less conscientious in waiting for possible excrement to appear. Nevertheless, the parents are still so eager to collect and remove droppings that I have frequently seen them diving in pursuit as a dropping fell earthwards from the nest.

Division of labour between the sexes. Basically, the mates seem to share the task of feeding the young about equally. However, the proportion of time allocated to feeding the nestlings at any particular time is mainly determined by the demand for female-specific duties on the nest. Only the female broods the nestlings, and when newly-hatched they require about the same attentive time as did the eggs, thus leaving the female with less time to devote to other duties. In the case of first broods, the male starts feeding the nestlings immediately after they have hatched, and in fact in both the nests studied the number of feeds for which he was responsible clearly exceeded those of the female (Figs. 2—3).

At the time of hatching of the second brood, however, the male may be still fully engaged in attending the young of the first brood. In consequence, the female alone has to cope with both the brooding and the feeding of the young of the second brood. During the first 4—5 days after hatching, the energy requirement of the nestlings is relatively low, however, viz. only about one feed per hour per nestling (Fig. 5), and the female apparently has no difficulty in finding sufficient food both for herself and for the young nestlings during her frequent periods off the nest, without having to sacrifice time usually spent brooding.

When the young of the first brood have become independent, after fledging, however, the male devotes more and more of his attention to those of the second brood. In the single case studied, although the last nestling of the first brood fledged on 7 July, the male attended this first offspring until 23 July, when the entire brood had finally left the territory. The hatching of the second brood began on 16 July and, as is clearly shown in Fig. 1, after a modest start on 16 July, the male had increased his share of feeding the nestlings in this nest to more than half of the total feeds by 23 July.

At any particular time the male's share of nestling feeding may vary from none at all to 100 %, the division of labour between the sexes depending on the current circumstances. I believe that the feeding patterns revealed in Figs. 1—3 are representative for this species. For the first brood (Fig. 2), the male's share in feeding increased throughout the entire nestling period, from about 4 feeds per hour at the start to about 15—18 during the latter part of the nestling period, whereas the female's contribution never exceeded 6 feeds per hour. It is noteworthy that when the female once almost stopped feeding the nestlings, during a 3-day period, the male quickly compensated for this shortfall by making extra visits to the nest with food. The reason for this fall in the rate of feeding by the female is quite clear. She was already busily preparing for the second brood and managed to finish laying a clutch of 8 eggs several days before any of the nestlings of the first brood fledged (Fig. 2).

With the other first brood studied, the male was once again the major food supplier for the nestlings, especially towards the end of the nestling period (Fig. 3). I suspect that in this case, too, the female was already preoccupied with her duties on a second nest, although I have no confirmatory data.

Fig. 1 shows the feeding pattern for the single second brood studied. As already mentioned above, until 23 July the male was busy feeding the offspring of the pair's first brood. From this date onwards, the pair had no parental duties other than looking after the second brood, and both parents took fairly equal shares in feed-

FIG. 8. A nestling 'shooting out' its excrement while clinging to the outside of the nest.

ing these nestlings, although the male's share was slightly greater (mean values for number of feeds per hour 6.6 and 5.2 for the male and female, respectively).

'Tremble-thrust' activities

When brooding the nestlings during daytime, the female frequently raises herself up and carries out 'tremble-thrust' movements. Standing in the nest cup she plunges her bill into the nest lining, whilst moving her head rapidly to and fro, often with such force that the whole nest quivers. This activity lasts for only a couple of seconds each time, but is usually repeated almost immediately, the successive bursts of activity forming a series of about 10—40 secs in duration (up to 2 1/2 min duration recorded). Each series of bursts is directed towards one or more places of 'attack', i.e. the female sometimes starts 'tremble-thrusting' close to the nest rim and then moves progressively downwards to the nest bottom, finally standing in an extreme head-down position (Fig. 9). Since she frequently turns sideways between successive bursts, in the course of time the whole circle of the nest is dealt with in this way.

'Tremble-thrust' activities seem to be linked with the brooding drive. At all events, I have never observed them after the time the female ceased warming the nestlings. To illustrate the frequency of this performance, I will cite an example selected at random. During a brooding period which lasted for 11 min (on the 8th nestling day), one female carried out 15 series of 'tremble-thrusts' altogether, each series lasting 6—46 secs, the entire

FIG. 9. The Goldcrest female in a head-down position, performing the 'tremble-thrust' movements in the nest.

activity time being 387 secs, or 59 % of the whole brooding period.

Discussion

It is quite normal for a Goldcrest pair to rear two overlapping broods each year. The parental investment in these broods must obviously be considerable, for the following reasons. Firstly, the Goldcrest builds an elaborate, well-insulated nest (one for each clutch), which involves a considerable amount of work, although both sexes cooperate in building it. Secondly, the female lays two relatively large clutches, of 9—11 and 8—10 eggs respectively, in the course of about two months. Thirdly, being the smallest European bird species (together with the Firecrest *Regulus ignicapillus)* its existence metabolism must be relatively high. Finally, the additional energy required for incubation presumably brings the female close to her limit of efficiency; incubating quite alone, she must collect all the food she needs without any help from the male, and maintain an egg mass weighing about one and a half times as much as herself at a mean temperature of about 36.5°C for a period of 16 days, under fluctuating environmental conditions (Haftorn 1978a).

In view of the presumably great energy cost of incubation (Haftorn 1978a), it is quite reasonable to think that natural selection favours birds which build well-insulated nests. Since such nests obviously involve a great deal of work to build, and the parental investment by the Goldcrest in general is appreciable, a high evolutionary premium will also be attached to good nest concealment. Typically, the Goldcrest's nest is well hidden within the needle network of the twigs, near the end of a long spruce branch (Fig. 10). Nest concealment is further improved by a camouflage of lichens, fastened to the outside of the nest.

Unfortunately, no reliable statistics for nesting success exist at present, but the predation rate is probably relatively moderate compared to that suffered by other open-nesters. It is difficult, otherwise, to explain either the low growth rate of Goldcrests or the relatively long-lasting nestling period (mean duration 19 days; Haftorn 1978c). The latter virtually places the species in the same category as hole-nesters, which have well-protected nests and a high breeding success compared to that of most open-nesters (Lack 1948, 1968).

In view of the presumably high energy demand of incubation, it seems puzzling that the Goldcrest has not evolved the habit of 'courtship feeding', especially as this feature is shown by its close relative the Firecrest (Thaler 1979), which definitely has a much more southern distribution than the Goldcrest. One may speculate whether 'courtship feeding' is perhaps incompatible with the strategy of overlapping double broods, at least in northern latitudes (the Firecrest, too, rears double broods, according to Glutz von Blotzheim (1962), but no detailed study of the division of labour between sexes has so far been made for this species). It may perhaps be too strenuous and 'complicated' for the male to attend two nests at the same time, i.e. to provide enough food for the well-grown young in one nest and for the incubating female in the second nest, the two nests being situated in separate parts of the territory. One may of course ask why the two broods have not become separated in time, so that the parental investment per unit time could be reduced. Strong selection pressure evidently exists for the overlap in time between the broods. One of the prime factors involved might be food availability. It is crucial for breeding success that the nestling and early fledgling periods, the times of maximum food requirement, coincide with the season during which an adequate food supply is most readily available. As also suggested previously (Haftorn 1978c), the period of optimal feeding conditions may be of limited duration, so that a time overlap between broods in fact enhances the chances of reproductive success despite involving a very high degree of parental investment within a short period of time. Furthermore, shortening of the period between fledging time and the start of the autumn might increase mortality among the juveniles, because they would have less time to reach maturity and gain experience before the time of migration, or of the worsening of the climate.

As postulated above, a reproductive strategy which involves the rearing of overlapping double broods makes a great energy demand on the parents, and consequently the degree of cooperation between the sexes most likely has a marked influence on the reproductive success.

One line of recent ecological thought considers that the two sexes are evolutionary competitors, implying that each sex will try to increase its inclusive fitness at the cost of the other (e.g. Krebs & Davies 1981). How does this idea fit the situation found for the Goldcrest? At one particular stage of the reproductive process it could be tempting for the male to quit and leave the rest of the parental duties to the female, namely the time when the juveniles of the first brood become independent and disappear from the territory. At this stage the male has just finished a particularly strenuous period, during which he fed a whole brood practically alone, during the latter part of the nestling period and the period of emancipation of the young outside the nest. However, instead of quitting, he straightway turns his attention to the second brood and takes an equal, or greater, share with his mate in feeding these nestlings.

FIG. 10. The Goldcrest female incubating. One twig covering the front of the nest was 'rolled up' before the photograph was taken.

The reason why the male 'chooses' to assist his mate is presumably that this strategy helps to maximize his inclusive fitness. To abandon the second brood would possibly markedly reduce its survival rate. Furthermore, there is, by then, certainly no time left for the male to find another mate and raise a third brood that year. His own chances of reproducing in the future may be somewhat diminished by staying with the second brood, but this is probably more than outweighed by the enhanced success of this brood. After all, the male's best chances of successfully passing on his genes to the next generation are possibly ensured by the strategy selected, which involves intimate cooperation with his mate throughout the reproductive season. In short, the observed strategy is evidently a matter of cost and benefit.

Theoretically, the Goldcrest could rear its two successive broods in the same nest and thereby save the energy expenditure involved in building a second nest. In fact, at least two cases of successive broods being reared in the same nest are known. Both were reported from Austria, where the two females in question started laying the second clutch 5 days after the first brood fledged (Thaler 1979).

Two successive broods in the same nest are evidently exceptional, however, as also pointed out by Thaler. One selection factor which would operate against it is the risk of transferring parasites from one brood to the next. The frequency of parasites in Goldcrest nests, however, appears to be negligible. It seems to me that time is the decisive factor which favours the rearing of overlapping broods, and that successive broods are disadvantageous, regardless whether they are reared in the same nest, or in two separate nests. It is noteworthy that the male may start to construct the second nest on his own, long before it is actually needed. The male of one pair was observed to start building the second nest at a time when the female was only on the point of finishing, or had just finished, laying the initial clutch in the first nest, 150 m away. As many as 33—34 days in fact elapsed between the start of building and the onset of egg-laying in the second nest (Haftorn 1978d). Thus, a major part of the work involved in building this second nest was done at a time when the male was relatively free from other reproductive duties.

According to my observations, the number of total feeding visits made to the nest increases with brood size, although not proportionally so (Haftorn 1978d). This contrasts with Thaler's (1979) findings. She concluded that the feeding frequency seemed to be independent of brood size. On the other hand, we both agree that, in principle, the male and female take approximately equal shares in feeding the young. Thaler mentions an exceptional case in which the male Goldcrest fed the nestlings only twice per hour, at most, during the nestling period, but shared the feeding duties equally with his mate after the nestlings fledged.

For just how long after leaving their nest are the juvenile Goldcrests still fed by their parents? Only a few data have yet been reported. Two first broods were fed within the territory, or its immediate surroundings, for at least 13 and 14 days after fledging (Haftorn 1978d). Thaler (1979) reports feeding periods of at least 12 and 14 days after fledging, respectively, for one first and one second brood of the same pair. After fledging, therefore, feeding by the parents generally seems to continue for about two weeks.

For a brood of Firecrests kept in captivity, Thaler (1979) observed two marked peaks in feeding frequency during the day, one in the forenoon and one in the evening. In my own Goldcrest investigations, the feeding visits were fairly evenly distributed throughout the day, though with a more or less distinct peak in the evening. However, in both our cases, the continuous records extended only over a period of two days, and therefore more data are required before a general description of the daily feeding rhythm can be given.

In a nest like that of the Goldcrest in which the nestlings are together during a period of nearly three weeks, there is a great need for maintaining hygienic conditions. All faeces are therefore carefully, and rapidly, removed by the parents. As is typical of passerines, Goldcrest defecation is linked with the feeding process. Instead of leaving the nest immediately after feeding the nestlings, the parents perch for a few seconds on the nest rim waiting for droppings. Young nestlings take much longer to defecate than do older ones. It is therefore essential that the parents adjust their waiting time to the age of the nestlings, and in fact they do so. Relatively seldom does it happen that nestlings defecate after the parents have left. It seems that, at each stage of nestling growth, the parents' waiting time is close to the time maximizing the 'reward' rate.

Towards the end of the nestling period this 'system' tends to fail, because the time spent waiting is cut too short. By this late stage of nestling development, however, the young are able to defecate outside the nest cup, independently of the parents' presence. Droppings which become stuck to the outside of the nest are soon removed by the parents, however, since they might increase the chances of discovery of the nest by predators.

'Tremble-thrust' activity is evidently common in birds. In the case of the Goldcrest this activity seems to be closely linked with the brooding drive. I have myself, at any rate, observed it only during brooding spells. This means that 'tremble-thrust' is an activity performed as long as the young are being warmed by the female, and not afterwards. There is apparently no need for this activity during the latter part of the nestling period.

The function of the 'tremble-thrust' activity is somewhat unclear, at least as far as the Goldcrest is concerned. The young certainly gradually take up more space in the nest as they grow, and it may be that the 'tremble-thrust' activity helps to widen the nest cavity. It may also keep the nest lining porous and thus maintain its insulating effect. A third functional possibility is that it serves to clear the nest of parasites or refuse. This problem is certainly an acute one for tits for example (own observations). In my experience, however, the Goldcrest is not markedly troubled with nest parasites, and if this were so, one would then expect the 'tremble-thrust' activity to be carried out throughout the nestling period, as in the case of tits.

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Selostus: **Hippiäisemojen osallistumisesta poikasten hoitoon**

Hippiäisellä on säännöllisesti kaksi, ajallisesti osittain päällekkäistä pesyettä vuodessa. Kirjoituksessa käsitellään emojen tehtävänjakoa poikasten hoidossa ja pyritään osoittamaan, että se on kehittynyt mahdollisimman tarkoituksenmukaiseksi kaksoispesinnän kannalta. Vain naaras hautoo ja lämmittää poikasia,

mutta molemmat emot osallistuvat pesän rakentamiseen ja poikasten ruokintaan. Koiraan ja naaraan ruokintateho kolmella eri pesällä on esitetty kuvissa 1—3 (1 = 2., 2 ja 3 = 1. poikue). Ensimmäistä poikuetta koiras ruokkii huomattavasti enemmän kuin naaras, joka joutuu aluksi lämmittämään poikasia ja loppuvaiheessa hautomaan toista pesyettä, kun taas toisen poikueen ruokinnasta naaras vastaa aluksi yksin koiraan vielä huolehtiessa ensimmäisestä poikueesta. Ruokintojen määrä lisääntyy poikuekoon kasvaessa (kuva 4) ja poikasten varttuessa (kuva 5). Ruokintateho pysyi kahtena tarkkailupäivänä melko tasaisena läpi valoisan ajan (kuva 6). Emojen ruokintaan ja ulosteiden poistoon käyttämä aika lyhenee poikasten iän mukana (kuva 7). Isot poikaset 'ampuvat' ulosteensa pesän reunan yli (kuva 8). Poikasia lämmittävä naaras tekee ajoittain väristysliikkeitä, pää pesävuoraukseen painettuna (kuva 9); tämän tehtävänä lienee pesäkupin laajentaminen poikasten kasvua varten. Pesätappiot ovat nähtävästi vähäiset pesän suojaisuuden ja naamioinnin ansiosta (kuva 10; pesän edestä yksi oksa käännetty ylös), mihin myös viittaavat poikasten hidas kehitys ja pitkä pesäpoikasaika (keskim. 19 vrk).

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