Nest-building by the Pied Flycatcher *Ficedula hypoleuca*

MONICA STJERNBERG

STJERNBERG, MONICA [Dept. of Zoology, University of Helsinki, P. Rautatiek. 13, SF-00100 Helsinki 10, Finland] 1974. — *Nest-building by the Pied Flycatcher* Ficedula hypoleuca. Ornis Fenn. 51:85—109.

The female Pied Flycatcher builds her nest of two types of material and with a restricted repertoire of fixed movements. In early stages of nest-building she brings more packing material than fibres to the nest, and a rough outer nest-layer is formed. As building progresses, the preference for fibrous material increases, finally reaching 100 per cent. The frequency of nest-building movements changes, and the female spends far more time in the nest at each visit. In this manner an inner layer composed mainly of fibres is formed. The actual lining of the nest-bowl is composed almost entirely of very fine fibrous material. The different phases of nest-building may be released by either stimuli from the nest or internal factors in the female, or both.

The external stimulus situation was modified in three sets of experiments, i.e. (1) removing the nest material daily, (2) providing narrower nest-boxes, (3) exchanging partly built nests for less or more completed ones. Through these experiments an attempt was made to clarify the relative importance of external and internal factors. The exchange experiments (set 3) were supplemented by a natural set of experiments, i.e. (4) Pied Flycatches building over nests of Great Tits.

The existence of external key stimuli, emanating from the nest, and influencing the Pied Flycatcher's repertoire of nest-building movements and preference for nest material was confirmed in all these four sets of experiments. But even so, internal factors played a role. For instance, the female did not go on building indefinitely in experiments (1). Phenomena like an abrupt decrease of building activity before the commencement of laying also testify to the existence of internal factors. The exchange experiments, and the cases in which the flycatchers built over the nests of Great Tits, showed that the flycatcher does not have to go through a fixed amount of nest-building to complete its nest, but can reduce its normal building activity considerably. However, in these experiments, the effect of internal factors was clear, as when some Pied Flycatchers building over a tit's nest did not reduce the amounts of material brought into the nest.

Contents

I. Introduction

a. Earlier studies

Nest-building in birds offers a classic example of a chain of fixed motor patterns leading to a definite result. Every link in the chain is released by the physiological situation of the building bird (internal factors) and/or by stimuli from the nest under construction (external factors).

Although the ornithological literature abounds in descriptions of birds' nests, very few detailed studies have been made on the technique of nest-building. For passerines, important work has been published by DECKERT (1955) on the lesser Whitethroat, the Blackcap and the Icterine Warbler, by the same author on the Great Tit (1964), on the Magpie (1968) and on the Starling (1970), by VAN DOBBEN (1949) on the Icterine Warbler and Chaffinch, by HINDE (1958) on the Canary, by KLUYVER (1955) on the Great Reed Warbler, by KRAMER (1950) on the Red-backed Shrike, by LÖHRL (1972) on the Blackbird, by MARLER (1956) on the Chaffinch, and by PALMGREN (1934) on the Goldcrest. Further TINBERGEN (according to THORPE 1963) has described the sequence of actions performed by the Long-tailed Tit when building.

Experimental studies on nest-building are even rarer. HINDE (1958) analysed the internal and external factors controlling the beginning, frequence, and cessation of the different nest-building movements, and the choice of different nest-materials in the Canary. COLLIAS and COLLIAS (1962) studied the nest-building mechanism in a weaverbird *Textor* or *Ploceus cucullatus* and were able, through ingenious experiments, to clarify the factors releasing the behaviour of the male and the female at every different stage of building.

In this connection a few experimental studies on the behaviour of other nest-building animals may be mentioned, as VAN IERSEL's (1953) classic study on the Three-spined Stickleback, and MELCHERS' (1964) experiments on cocoon-building in spiders.

The nest and nest-building mechanisms of the Pied Flycatcher have so far only been discussed briefly, e.g. by CAMPBELL (1950), CREUTZ (1937, 1955), CURIO (1959), VON HAARTMAN (1959), VON HAARTMAN et al. (1963—1972), MEIDELL (rewritten by VON HAARTMAN, 1961), NÖHRING (1943, in captivity), and ZIMIN (1972).

The Pied Flycatcher is in many respects a favourable species for an experimental study of nest-building. It is easily attracted by nest-boxes and tolerates considerable changes in the nest. Nest-boxes may, for instance, be replaced by others containing more or less nest material than the original. The sexes are easy to distinguish, and the females do not desert if taken from the nest and ringed for the purpose of identification.

The present study is a shortened version of the author's dissertation for a master's degree in zoology (1968). Of the numerous original tables and histograms only part are included. The text has been adapted for printing and translated by Lars von Haartman.

b. Study area and data

The study was carried out on Svartholmen and Löparö, islands in the commune of Sibbo, southern Finland. On Svartholmen the area studied was 3.5 ha, on Löparö 10 ha. The two islands form part of the inner archipelago. The vegetation in the study area is mainly coniferous forest of *Oxalis-Myrtillus* to *Myrtillus* type, on Svartholmen locally interrupted by pine forest on rocky ground, on Löparö by meadows. On Löparö, there is considerable interspersion of birch, which was reflected in the composition of the nest-material of the Pied Flycatchers.

The study was carried out in the years 1963—1965 and 1967. The first males arrive at the end of April to beginning of May, and the females somewhat later (VON HAARTMAN et al. 1963—1972). Regular field work was commenced on May 12 1963, May 11 1964,

TABLE 1. Number of nest-boxes and population of Pied Flycatchers on Svartholmen and Löparö.

	A Nest-boxes	B Occupied *	C Occupied by Pied Fly-catchers *	D C in per cent of A	E C in per cent of B
1963	54	28	20	37	71
1964	62	32	17	27	53
1965	60	42	17	28	41
1966	60	28	14	23	50
1967	60	30	14	23	47

* At least one egg laid.

May 8 1965, and May 17 1967, and continued for 4—5 weeks, i.e. as long as nest-building was going on.

All nest-boxes were of identical dimensions and appearance (floor 12.5 times 8.5 cm, height 23.5 cm, entrance diameter 3.2 cm). The roof could be pushed sideways to permit inspection. Every autumn and spring the boxes were emptied of nest-material and excreta of roosting Great Tits. The number of nest-boxes and the development of the population is shown in Table 1.

In spite of the increased number of nest-boxes, the population of Pied Flycatchers decreased. A few nest-building females left the area as a result of the experiments, and this may slightly have reduced the number of breeding females. In 1966, however, even though no experiments were carried out, there were fewer breeding females than in any other year except 1967. The Great Tit was the Flycatcher's most serious competitor for nest-boxes. In a few cases Pied Flycatchers built their nests over those of tits, a situation of special interest for the present study.

In all, the structural features of 16 nests that were not influenced by any kind of experiment were examined. Three of these were built over nests of the Great Tit, and the other 13 ("standard nests") were begun in empty nest-boxes. In addition, the composition of 21 nests built under varying experimental conditions was analysed. At 2 nests building was followed continuously from a hide with a view into the nest-box.

II. Description of the nest and nest-building

a. Composition and architecture of the nest

The statement frequently made in the literature that there are two distinct layers in the nest of the Pied Flycatcher is mainly correct, although the border between the outer and inner layers (Fig. 1) is less sharp than is usually maintained. In the present study the border between the layers was determined subjectively. In two nests, a third, transitional, layer, consisting of long, unwieldy grass-straws, seemed to exist between the other two.

The outer layer is mainly composed of packing or filling material, whereas in the inner layer fibrous or straw material predominates. The lining of the nest-cup, which is built last and forms the most carefully constructed part of the inner layer, is almost without exception composed of fine grass, animal hair, and spore capsule shafts of moss.

The p a c k i n g m a t e r i a l consists mainly of bulky pieces of such items as thin flakes of pine and birch bark, dead leaves, bast fibres, beard lichen, moss, and pine needles. Pine needles, although not bulky, cannot be regarded as fibrous material.

— Thin flakes of bark from the upper parts of pine trunks, usually flat and rectangular, occurred in every nest examined, often amounting to several hundred.

— Flakes of birch bark, paper thin, often longish and coiled, occurred in all nests and quantitatively replaced the flakes of pine bark in habitats where birch dominated.

— Dead leaves, mainly of birch and alder, sometimes sallow, aspen, *Ribes alpinum, Vaccinium myrtillus,* and *Pteridium aquilinum,* with the flakes of pine and birch bark, form

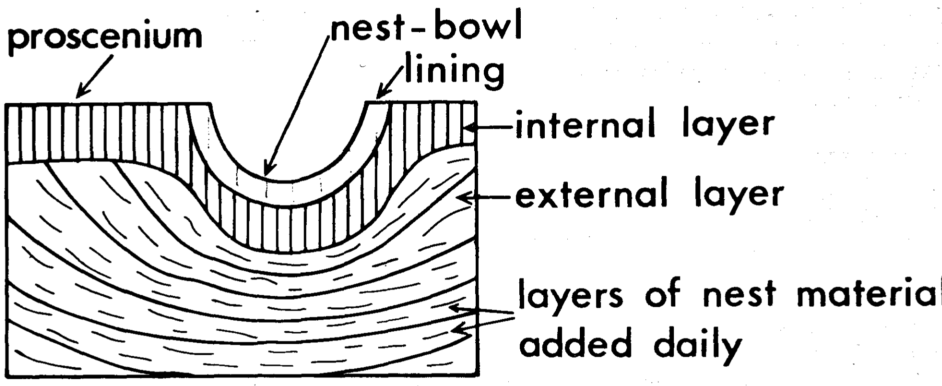


FIG. 1. A diagram of the nest of the Pied Flycatcher.

the bulk of the packing material, and were present in every nest.

— Bast fibres, up to 25 cm long, flexible, not infrequently a cm broad, often split up at the edges, were taken from trunks and branches of juniper, spruce, and *Potentilla fruticosa,* which was planted in a garden in the area. Bast fibres occurred in the majority of the nests, often in considerable numbers.

— Beard lichen, large pieces of *Usnea* sp. or *Alectoria* sp., often with conifer needles attached, in which case the entire agglomerate was considered as one item, were found in most of the nests, although always in small quantity.

— Moss, pieces of mosses such as *Hylocomium splendens, Pleurozium Schreberi,* etc., but never *Sphagnum,* were found in small amounts in most nests.

— Pine needles occurred in most nests, but only in small numbers.

— Occasionally the nests contained some dry spruce twigs, devoid of needles, and in addition spruce needles. Fragments of such tree lichens as *Parmelia* and *Evernia,* grass panicles and grass shoots with the roots attached, fruit sprigs of herbs, plastic, down and feathers, scales of cones, stems of dwarf-shrubs, twigs of juniper, cobwebs with seeds attached, catkins, and tendrils.

The f i b r o u s m a t e r i a l is relatively long, thin, and flexible. The main types were:

— Dry stalks and blades of last year's grass, up to 40 cm long, were present in large amounts in all nests.

— Stalks of moss spore capsules were taken from mosses of different kind. They have a characteristic copper colour and are often used to line the nest bowl.

— Elk hairs and horsehair. The Pied Flycatcher is incredibly skilful in finding animal hair, which forms an excellent nest lining. In a single nest over 800 elk hairs were counted! Hairs from horses' tails were found in only three nests, there being a horse only on Löparö.

— Plant fluff, sewing-cotton thread, and human hairs were exceptional components.

In the nests, examined by V. Rosengren (personal communication) in western Finland, root fibres played a considerable part. They were never found in the nests on Svartholmen and Löparö. Roots as nest material are also mentioned by CREUTZ (1943 and 1955), CURIO (1959), and MEIDELL (1961). CREUTZ (1955) maintains that moss and animal hair only occasionally occur in nests of the Pied Flycatcher.

In all the nests there was a certain amount, c. 5—10 (20) per cent by weight, of fragmentary material. This material has been disregarded, except when the total weight of the nests are given.

The occurrence of different materials in standard nests of the Pied Flycatcher is shown in Table 2.

TABLE 2. Occurrence of packing and fibrous material in 13 standard nests of the Pied Flycatcher. Brackets indicate that the material in question was found in one or more of the other 24 examined nests but not in the standard ones.

	Number	Per cent		Number	Per cent
Packing material					
Thin flakes of pine bark	13	100	Down feathers	1	8
Leaves	13	100	Feathers	1	8
Pine needles	10	77	Bilberry twigs	1	8
Flakes of birch bark	8	62	Plastic	1	8
Moss	7	54	Grass panicles	( )	
Beard lichen	7	54	Fruit sprigs	( )	
Spruce twigs	4	31	Catkins	( )	
Grass roots + stems	3	23	Pieces of string	( )	
Lichen	1	8	Tendrils	( )	
Dwarf shrub stems	1	8	Flower springs	( )	
Cobwebs + seeds	1	8	Cone scales	( )	
Juniper twigs	1	8	Spruce needles	( )	
Fibrous material					
	Number	Per cent		Number	Per cent
Grasses	13	100	Horsehair	1	8
Elk hair	6	46	Plant fluff	1	8
Stalks of moss spore			Human hair	1	8
capsules	1	8	Sewing-thread	( )	

As a nest-builder the Pied Flycatcher is an opportunist. The material it collects depends largely upon what is available in the vicinity of the nest (cf. also MEIDELL 1961).

The numbers and weights of the pieces of packing and fibrous material in the standard nests are shown in Table 3.

The mean weights of the pieces of material in the two layers were:

Packing material	
Outer layer	0.024 g
Inner layer	0.022 g
Fibrous material	
Outer layer	0.011 g
Inner layer	0.005 g

As the figures clearly show, the fibrous material in the outer layer is much bulkier than the finer grass in the inner layer. It functions as fibrous and packing material at the same time.

b. Duration of the nest-building period

In none of the standard nests was building observed after the laying of the first egg (cf., however, observations to the contrary by ZIMIN 1972). But on the very morning when the first egg is laid, a little material may still be carried in. Sometimes the nest seemed to be quite complete 1—3 days before the first egg was laid. Even during these days some finer fibrous material may possibly

TABLE 3. Average numbers and weights of the pieces of packing (A) and fibrous (B) material in 13 standard nests of the Pied Flycatcher.

Outer layer				Inner layer			
Numbers		Weight (g)		Numbers		Weight (g)	
A	B	A	B	A	B	A	B
481	344	11.55	3.67	102	431	2.22	1.96
58 %	42 %	76 %	24 %	19 %	81 %	53 %	47 %

TABLE 4. Duration (in days) of the nest-building period in 13 standard nests.

Period	4	5	6	7	8	9	10	11	Mean
First nests	—	—	1	1	3	—	1	1	8.3
Replacement nests	4	1	1	—	—	—	—	—	4.5

have been added to the nest, but this is not likely, considering the large number of nests which, when apparently complete, remained without eggs for one or more days (cf. MEIDELL 1961). CREUTZ (1943) maintains that nests may be completed as much as 8 days before laying.

A few females carried single pieces into the nest-box 1—2 days before the commencement of nest-building proper. For practical reasons, this material was included with that carried in on the first day of intense building, "day 1". The nest-building period was calculated from the first day of intense nest-building till the last day on which nest-building was observed. In the nests under observation, the length of this period varied between 4 and 11 days (Table 4).

Replacement of a nest, in the above cases, was caused by my interference with the first nest, whereupon the pair moved to another nest-box in the neighbourhood.

According to CURIO, the nest-building takes 2—9 days, averaging 5 days.

The outer layer, according to my observations, was finished in 1—3 (5) days, the average for 13 standard nests being 2.2 days (7 first nests 2.4 days, 6 replacement nests 1.8 days). CREUTZ's (1943) figures for the outer layer (4—8 days, exceptionally 1—2 days) are not fully comparable to mine, as he defined this layer somewhat more widely.

The inner layer was usually built in 2—6 days, but exceptionally took up to 9 days. The average for 13 standard nests was 4.2 days. Of these, 7 were first nests (average 5.6 days), and 6 replacement nests (average 2.7 days).

c. Nest weight

In spite of the considerable variation in the length of the nest-building period, the weights of the finished nests in the standard nest-boxes varied little (Fig. 2).

The difference between the first and replacement nests is not statistically significant (Student's t-test). The fact that nests built during a longer period were but little heavier shows that the average amount of material, added to the nest daily, was inversely correlated with the length of the building period.

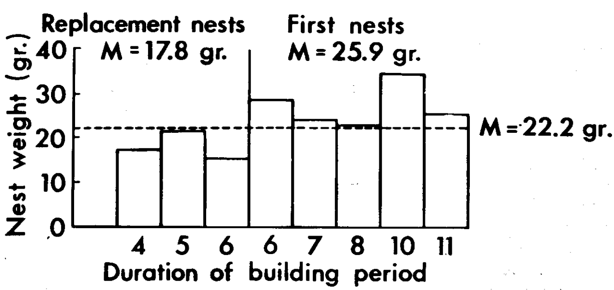


FIG. 2. Weight of 13 standard nests, including crumbled nest material. If several nests were built during the same number of days, the figure denotes the average.

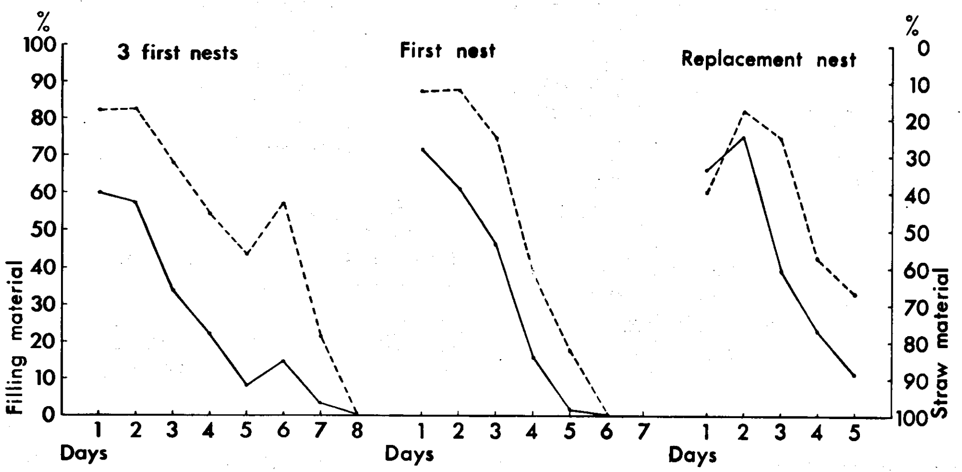


FIG. 3 a—c. Material added daily to five nests of the Pied Flycatcher. --- = weight, ——— = numbers. The histogram showing nest-building activity during 8 days (a) is based on average values for 3 nests of different birds.

d. Changes in preference for nest material during the building period

The material brought into the nest daily was made recognizable by placing different-coloured threads over the nest at the end of every day. These threads were only exceptionally removed by the bird, in which case the material collected during two days was split evenly between the two days. Fig. 3 a—c shows the proportions of packing and fibrous material added to the nest daily in five representative cases.

On the first day of nest-building (13 standard nests) the number of items classified as packing material, amounted to 64 per cent. This figure decreased continuously and on the last day amounted to only 4 per cent. In first nests the average decrease was more rapid, from 71 to 0 per cent, in replacement nests from 57 to 7 per cent.

The percentage of fibrous material increased correspondingly from 36 to 96 per cent (13 nests). In first nests the increase was from 29 to 100 per cent, in replacement nests from 43 to 93 per cent.

The relative weights of packing and fibrous material brought to the nest daily (Fig. 3) are fairly similar to their relative numbers. According to HINDE's (1958) study on the Canary, numbers and weights do not necessarily depend upon the same factors, but in the Pied Flycatcher this is probably the case.

In replacement nests the numbers and weights of the fibrous material did not reach 100 per cent even on the last day of building. This indicates that the female is in a hurry to lay, and so leaves her second nest in a somewhat less complete state than the first.

The daily change in the relative importance of the two kinds of nest material might evidently be related to the absolute weight of the material in different ways:

(1) The female might gradually come to prefer fibres to packing material.

(2) The amount of packing material might decrease, while the amount of fibrous material remained constant.

(3) The amount of both materials might decrease, the amount of fibrous material decreasing more slowly.

(4) The amount of both materials might remain the same from day to day, the lighter

fibrous material "floating" up as the female performed building movements. This alternative can immediately be discarded, as the material added daily was known, and the fibrous material did not pass through the layers added on subsequent days.

The absolute amounts, both by number and weight, of packing and fibrous material carried daily into three representative nests is shown in Fig. 4.

The weight of the material carried into the nest was maximal during the first to third days of building. In 5 nests the maximum was reached on the first, in 7 nests on the second, and in 1 on the third day of building.

If we consider only the weight of the packing and fibrous material, alternative (3) above seems to be fulfilled, i.e. the amounts of both kinds of material decrease as building progresses, the amount of packing material decreasing more rapidly. The total number of pieces brought into the nest shows a maximum coinciding with the maximum weight. The number of pieces of packing material reaches its maximum 1—2, seldom more, days before the number of pieces of fibres. Towards the end of the building period, the number of fibrous items is much higher than the number of packing items. We thus arrive at the conclusion that the inner layer arises through a combination of alternatives (1) and (3) above. The female gradually comes to prefer fibrous to packing material, after which a phase is reached when the amounts of both kinds of material decrease, but the amount of fibrous material much more slowly.

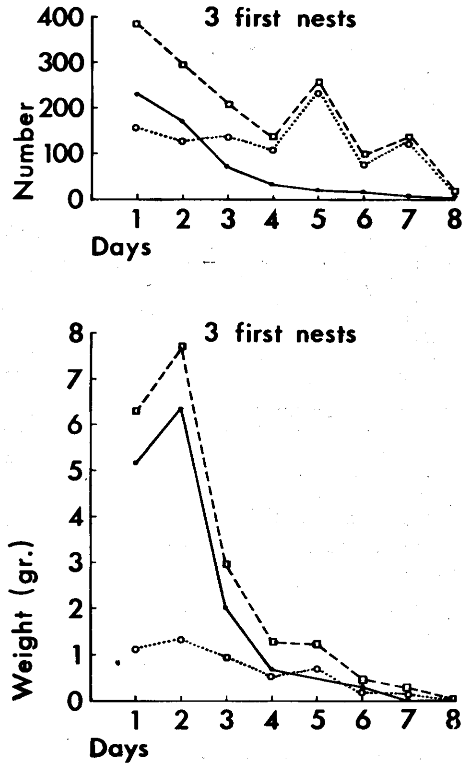


FIG. 4. Average numbers and weight of packing and fibrous material added daily to 3 first nests built during 8 days. □---□ = total number and total weight, ○····○ = number and weight of fibrous material, ●——● = number and weight of packing material.

e. Collecting technique

The Pied Flycatcher builds most actively from early in the morning to c. 10—11 a.m. A little building activity sometimes occurs in the afternoon, but for practical reasons no observations were carried out at that time.

Only the female was seen collecting nest material, carrying it into the nest-box, and performing nest-building movements inside it. NÖHRING (1943) reports that in a few cases the male in captivity took part in the building with the female from the beginning or from the 7th day on, the ratio of male to female work being 2:11. During the building period the male may visit the nest-box and, especially in the first few days, continue his pair-forming display at the nest-box, but under natural conditions he was never seen to build.

Twice, the male was seen carrying out thin flakes of pine bark from the nest-box. The female may also carry out nest material, e.g. grasses that are too long and leaves and thin flakes of pine bark that are too large (cf. von Haartman 1952 on the Pied Flycatcher, and Löhrl 1951 on the Collared Flycatcher).

The collecting technique of the female (cf. also Curio 1959) was studied with field glass. All females observed by me searched for material in the close vicinity of the nest. Rosengren (personal communication) saw the female searching for nest material up to 50 m, and von Haartman (1956b) up to 100 m from the nest. The main collecting methods were:

— The female, fluttering in front of pine and birch trunks, took loose flakes of bark either from the trunk or when they whirled in the air.

— The female plucked last years' alder leaves directly from the branches and from the ground.

— The female stood on the ground tearing bast fibres off the lower parts of the stem and lower branches of a planted clump of *Potentilla fruticosa*.

— With her bill the female tore dry grass from the ground. Large pieces were carried single to the nest, smaller ones in bunches.

Because of the small diameter of the entrance, larger flakes of pine bark were often fragmented, some falling down, others being carried in.

The female usually jumps with the material to the floor of the nest. Here she drops it, nearly always at the hind wall of the nest-box or at one of its hind corners.

Bulky material may get caught in the entrance. Sometimes the female pushes it in from the outside without entering the nest-box. Once, when this technique did not succeed, the female jumped in and drew in the material (cf. also Curio 1959). Four times during the building period the female was seen to visit the nest-box without bringing in any material. At these visits she performed building movements inside the nest-box. Kramer (1950) observed that Red-backed Shrikes with nearly complete nests paid frequent visits to the nest for the sole purpose of performing nest-building movements; no material was carried in.

f. Nest-building technique

Observations were made from a hide, to the front of which was attached a standard nest-box. The interior of the nest-box was visible through a "door eye" of the type commonly used at the front door of apartments and permitting unidirectional vision. These observations were carried out on May 24—26 1963 and May 15—21 1964, from about 3.50 a.m. until nest-building had ceased for at least an hour, in no case, however, later than 1.30 p.m.

The female may bring material to the nest-box, and then leave immediately. More often she stays and performs nest-building movements. These are of three kinds: (1) scratching backwards with the feet, (2) tamping in material with the wing or wings, and (3) plucking with the bill.

Building with feet and breast. Scratching (see also the description given by von Haartman 1959) is the most important of these movements. After depositing the material, the female lies down, usually with her bill on the piece of material just brought in, her wings somewhat abducted, her breast pushed against the substratum, and her tail pointing slightly upwards. In this position she swiftly scratches backwards a number of times, alternately with both feet. Then she rises and either jumps out or lies down again, in the same direction or another, and repeats the scratching. I have seen a female perform up to 18 such scratching bouts during a single visit to the nest. As a result of the scratching, the nest material is thrown against the walls of the nest-box. It is spread more or less uniformly in all directions, as the female usually turns before she scratches again. At longer visits (1—2 min.) she has time to turn a couple of times through 360° in this manner.

Scratching is performed from the very beginning of nest-building, even when the nest-box is empty. The female lies down in the empty nest-box with the piece of nest material ahead of herself, possibly pushing it down with her bill, and kicks backwards with her legs. This behaviour shows how stereotyped the nest-building movements of the Pied Flycatcher are. There has evidently been an adequate initial stimulus (the nest material brought into the nest-cavity), and this releases a fixed chain of movements, which seemingly continues "in vacuo".

The female often removes single pieces of nest material, which stand up at the proscenium of the nest (cf. Fig. 1), and which she has tried in vain to draw under herself with her bill. In this case, visual stimuli obviously release the reaction. VON HAARTMAN (1952) found that tactile stimuli may release removal of nest material from the nest-bowl in incubating females.

In the beginning, as a consequence of the scratching, the nest material concentrates round the walls of the nest-box. Long items come to lie horizontally, so that the material assumes a circular arrangement (cf. DECKERT 1955 and KRAMER 1950). As nest-building progresses, the floor of the nest-box becomes covered with material. In spite of the scratching no regular nest-bowl is formed to begin with, merely a shallow depression. A distinct nest-bowl arises only when more fibrous material has accumulated. The main reason why a nest-bowl is formed only in the later stage of nest-building is that fibrous material is more malleable than packing material, and, further, that the building female's behaviour changes during the nest-building period (Fig. 5).

Fig. 5 shows that both the duration of visits to the nest and the frequency of nest-building movements increase strongly after the third day of building, i.e. when the outer layer is finished, reaching a maximum on the penultimate day of building (cf. also NICE 1964). An especially striking feature is the increased use of the bill in the later phase of nest-building. Towards the end of the building period "tidyings" of the nest also occur, when, between scratching bouts, the female with her bill removes all the protruding pieces it detects. Visits spent in tidying usually lasted 1.5—2 minutes, whereas ordinary visits, including a single scratching bout, lasted only 4—14 seconds.

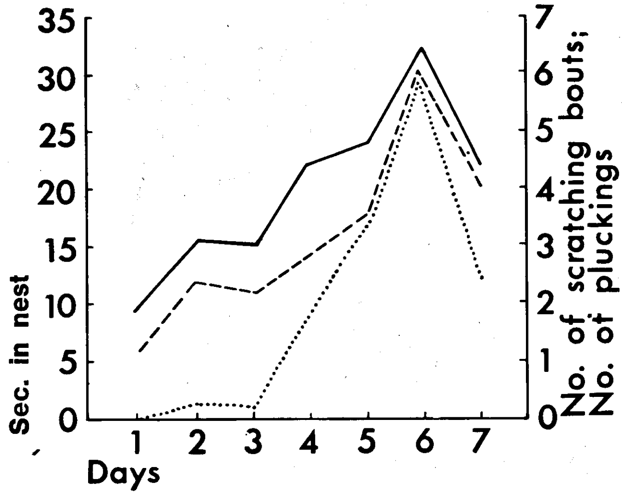
Building with the wings. When scraching, the female keeps her wings somewhat abducted. This causes the nest material of the proscenium to become pressed down, so that it gets a smooth upper surface. Repeatedly, I have seen the female lift one or sometimes both wings over a protruding piece of nest material on the proscenium, pressing it down.

Building with the bill. The female plucks protruding pieces of packing material, especially thin flakes of bark and leaves, removing them from the proscenium of the nest to the bowl below her breast. With the aid of the breast this material is then pressed down. In this way, the fibres become twisted into the nest so that the rim of the nest-bowl becomes very firm (Fig. 6).

If, in spite of repeated attempts, the female does not manage to "trim" a certain item of material, she usually sooner or later carries it out.

Whereas scratching in different directions causes the nest material to accumulate round the bird, the body, especially the breast of the bird, presses material down into a smooth bowl. The bowl keeps its form in spite of the loose construction of the nest material, partly as a consequence of the circular arrangement of the fibrous material, partly

FIG. 5. — = average time (in sec.) of visits of the female to the nest on different days of building, - - - = number of scratching bouts per nest visits, · · · · = number of pluckings per nest visit.



thanks to the turning of the protruding ends of fibres of the proscenium into the nest-bowl (cf. the rapid increase in numbers of plucking movements with the bill in Fig. 5).

The nest bowl was nearly round (average length in 13 nests 60 mm, and breadth 57 mm) the depth being less than the diameter (in 10 nests averaging 43 mm). It was closer to the hind wall than to the front wall of the nest-box, and midway between the side walls. In 12 nests the distance from the rim of the bowl to the front wall averaged 50 mm, to the hind wall 17 mm. This position is in accordance with CAMPBELL's (1950) and VON HAARTMAN's (1959) descriptions, whereas CURIO (1959) and CREUTZ (1937) maintain that the nest-bowl is closer to one or other of the hind corners of the nest-box. VON HAARTMAN (personal communication) saw this asymmetrical position only in a very large nest-box, where light came in from both the entrance and a slit in one side; the nest-bowl was placed at the corner most distant from the source of light.

Why is the nest-bowl placed at the hind wall of the nest-box? The female practically always places the nest material at the hind wall. Thereafter she pushes the material against the floor with the bill. This starting position repeats itself from visit to visit. The place of the female's feet will form the centre of a circle, where her breast is the radius. DECKERT (1955) observed that the Lesser Whitethroat always arrived from the same direction, usually delivering the nest material ahead of itself. As a result, the side of the nest

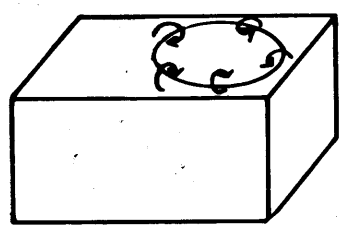


FIG. 6. Diagram of the construction of the rim of the nest-bowl. The arrows show how protruding fibres are turned towards the middle, where the bird's breast presses them down.

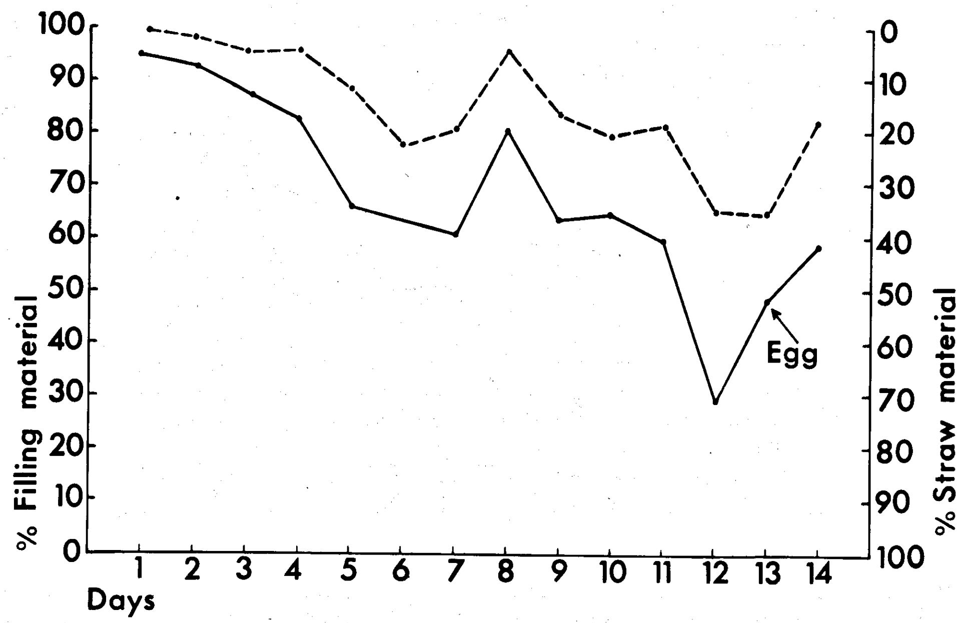


FIG. 7. Proportions of packing and fibrous material brought daily to a standard nest-box, where the material was removed every evening. - - - weight, ——— numbers. Egg = first egg laid.

opposite to the direction of arrival became denser than the rest of the nest. However, this was not the case with the Pied Flycatcher.

III. Experimental study of nest-building

a. Continuous removal of nest material

The standard nests contained an average of 43 per cent of packing and 57 per cent of fibrous material. The outer layer was usually composed of somewhat more packing material, whereas fibrous material dominated in the inner layer. The amount of material carried in daily decreased continuously after a maximum on the first to third days of nest-building, and ceased completely as soon as the first egg was laid.

In three sets of experiments the role of internal versus external factors in determining the course of nest-building was tested by changing the external stimulus situation.

In one set of experiments the material brought to the nest-box during the day time was removed every evening. This was done in nine nest-boxes. In three of them the female deserted the nest, in six she continued to build, and finally laid eggs.

If the choice of nest material and the length of the building period are determined entirely by internal factors, the female should, in spite of removal of the material, build in the same way as in intact nests, i.e. bring less and less material composed more and more of fibres. But if the course of nest-building is determined by external factors, the female should build as if every day were the first building day.

The female may prolong her building period if the nest material is continuously removed. The observed maximum

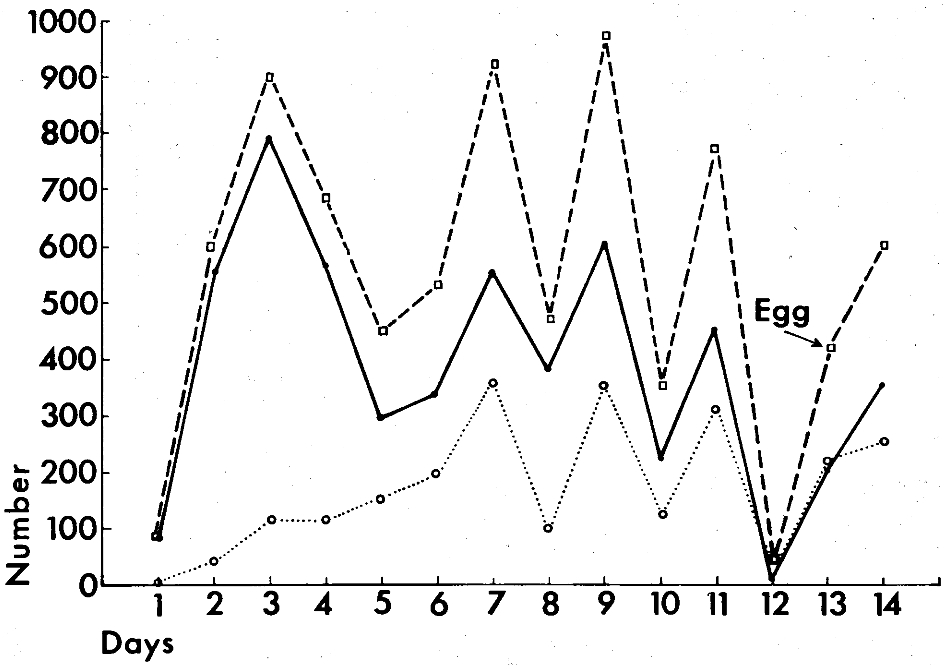


FIG. 8. Numbers of packing and fibrous items, brought daily to a standard nest-box, where the material was removed every evening. ···· = packing material, ——— = fibrous material, - - - total numbers. Egg = first egg laid.

was 14 days. Two females built for 9, one for 8, and two for 6 days, averaging 8.7 days (in standard nests 4—11, averaging 6.5 days; in first standard nests, however, 8.3 days on the average). In three nests the first egg was laid on very little nest material (e.g. Fig. 7—9). In two of these nests the female continued to build one or more days after she had started to lay, a phenomenon never observed in non-experimental circumstances. CURIO (1959) mentioned a female whose nest material was almost completely removed by Wrynecks and who laid her eggs on the bare floor of the nest-box within a meagre ring of nest material, and ZIMIN (1972) maintains that egg deposition may occur before nest composition, late in the season even on the bare floor.

The weights and numbers of pieces of packing material and fibres in the six nests from which material was continuously removed changed from a mean of 86 per cent packing material on the first day to 66 per cent on the last day of building. In the first standard nests the corresponding figures were 71 and 0 per cent. The weight and numbers of pieces of packing material collected daily in the experimental nests remained almost constant throughout the building period. In the standard nests it decreased after a maximum reached in one of the first three building days. The weight and numbers of fibrous items remained relatively constant. In consequence, when the building material was removed, the ratio of the two components (Fig. 7) changed relatively little during

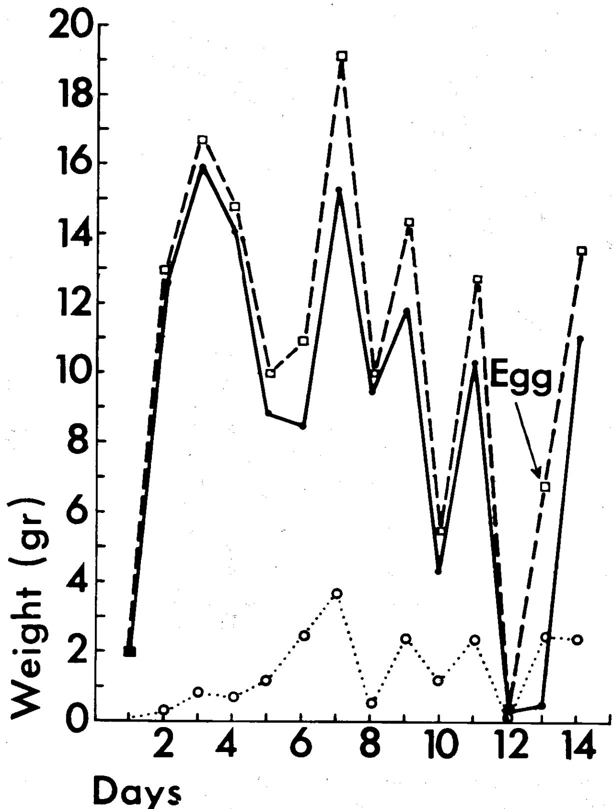


FIG. 9. Weight of packing and fibrous material, brought daily to a standard nest-box, where the material was removed every evening. ···· = fibrous material, ——— = packing material, --- = total weight. Egg = first egg laid.

the building period. In these experiments, the Pied Flycatcher built almost, although not quite, as if every day were the first day of building. This is also shown in Table 5. In the removal experiments the average daily weight of material carried into the nest-box was nearly three times, and the total weight four times as much as in normal nest-building.

Canaries whose nests were removed daily carried in c. 2.5 times as much material as Canaries whose nests were not removed (HINDE 1958).

When the nest material was removed daily, the pieces of fibrous material remained of almost identical weight throughout the building period (Fig. 10). In the standard nests, in contrast, their weight decreased continuously after the first 2—3 days of building. The females, forced to start anew every

TABLE 5. Mean weight of material (in g) in standard nests and nests from which the material was removed daily.

	Number of nests	Total weight Range	Mean	Daily mean
Removal experiments	6	46.3—164.0	85.1	9.5
Standard nests	13	13.1— 34.3	22.2	3.6

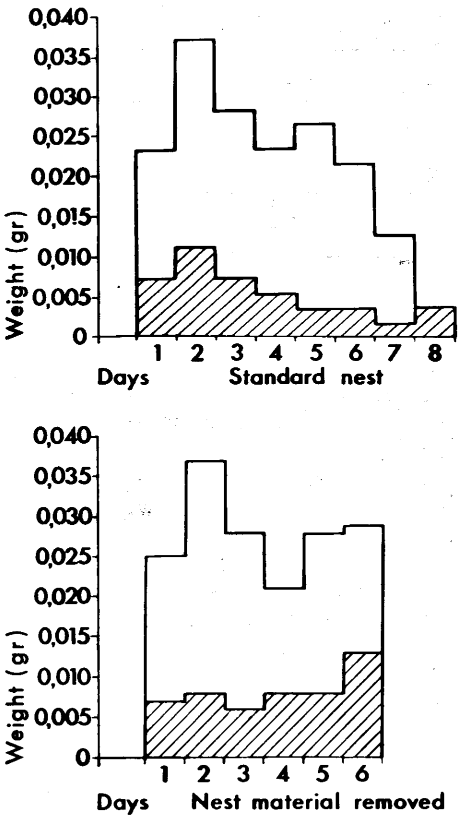


FIG. 10. Weight per item of nest-material in a standard nest and in a nest, from which the material was removed daily. ☐ = packing material, ▨ = fibrous material.

morning, never arrived at the final stage of building, nest-lining.

These experiments indicate that the Pied Flycatcher adapts itself to the actual situation in the nest-box. When nest-building is undisturbed, the use of packing material is obviously inhibited as the nest approaches completion. Under natural conditions the nest acts as a regulator of both the amount and nature of the material carried in. In the removal experiments, this regulatory process was suppressed.

The observations that, if the nest is continuously removed, the female does not build indefinitely, and that the ratio of packing material to fibrous material undergoes a continuous, if weak change, indicate that internal factors do play some role. The almost complete cessation of building the day before the start of egg-laying in one of the nests points in the same direction (Figs. 8, 9).

b. Nest-boxes of reduced size

A series of experiments was carried out in which the cross-section of the nest-box was reduced either by placing loose boards at the hind wall of the box, or at the hind wall and one or both of the side walls. Whereas the standard nest-boxes were 106 sq. cm in cross-section, the nest-boxes of reduced size were 77—97 (average 86) sq. cm.

Nest-boxes with a cross-section of less than 70 sq. cm were not accepted by my Pied Flycatchers. In areas where there is great shortage of nest holes, however, the species may nest in very narrow cavities. In a Norwegian field area, for instance, the Pied Flycatcher nested in considerable numbers in old nests of the Willow Tit in birch stumps (MEIDELL 1961).

If the amount of building material is determined by internal factors, nests built in narrow nest-boxes ought to be as heavy as nests in standard nest-boxes, though much deeper. In fact (Table 6)

TABLE 6. Weight and depth of nests in nest-boxes of reduced cross-section as compared with standard nests.

Nest	Number	Cross-section (sq. cm)	Building period (days)	Depth of nest (cm)	Weight of nest (g)
Standard	12	106	(4) 7 (11)	(6.0) 7.6 (12.0)	(13.1) 22.2 (34.3)
Reduced	8	(77) 86 (97)	(6) 7 (8)	(6.6) 7.8 (11.3)	(13.8) 19.6 (26.4)

TABLE 7. Amount of packing (A) and fibrous (B) material in nest-boxes of reduced cross-section as compared with standard nest-boxes.

	Standard (n = 13)				Narrow (n = 8)			
	Number		Weight (g)		Number		Weight (g)	
	A	B	A	B	A	B	A	B
Outer layer	481	344	11.55	3.67	610	480	10.82	3.15
Inner layer	102	431	2.22	1.96	70	544	1.43	1.93

the depth of the experimental nests was the same as the depth of the standard nests, and the experimental nests were therefore lighter (an average of 2.6 g lighter than the standard nests, and 6.3 g lighter than first standard nests).

According to CREUTZ (1955) the Pied Flycatcher builds deeper nests in very deep holes, and this is also true of the Great Tit (HINDE 1952). These observations imply that both species adjust their nest-building to the actual situation.

Table 7 shows the components of the nest in standard and narrow nest-boxes.

In nest-boxes of reduced cross-section the pieces of nest material in the outer layer were more numerous than in the standard nest-boxes, though their weight was less. With other words, in narrow nest-boxes the female used smaller pieces of material for the outer layer (Table 8).

The relative amounts of packing and fibrous material in standard and narrow nest-boxes are exemplified in Figure 11. At first sight it may seem odd that the histograms for the two types of nest-boxes are so similar. One would, perhaps, expect the female in narrow nest-boxes to switch sooner from building the outer layer to building the inner one. The reason, or one of the reasons, why this is not so, is that the bird uses smaller pieces of material in narrow nest-boxes. The duration of the nest-building period thus remains unchanged, and the corresponding phases of nest-building are reached as slowly in narrow as in standard nest-boxes.

c. Exchange of nests at different stages of completion

Eight nest-boxes in which the Pied Flycatcher had just started to build or where the nest was at most half built, were replaced by nest-boxes in which the nest was half built to complete. Three nests again were exchanged for less complete ones. The exchanges were made in the evening.

The female can be expected either to continue to build as if no interference had taken place (internal factors directing behaviour), or to adjust her building activity to the new situation, bringing less material to a more advanced exchange nest, and more material to a less advanced exchange nest.

The results of the exchange experiments are summarized in Tables 9 and

TABLE 8. Mean weight (in g) of items of packing (A) and fibrous (B) material in standard nest-boxes and nest-boxes of reduced cross-section.

	Standard		Reduced	
	A	B	A	B
Outer layer	0.024	0.011	0.018	0.007
Inner layer	0.022	0.005	0.020	0.004

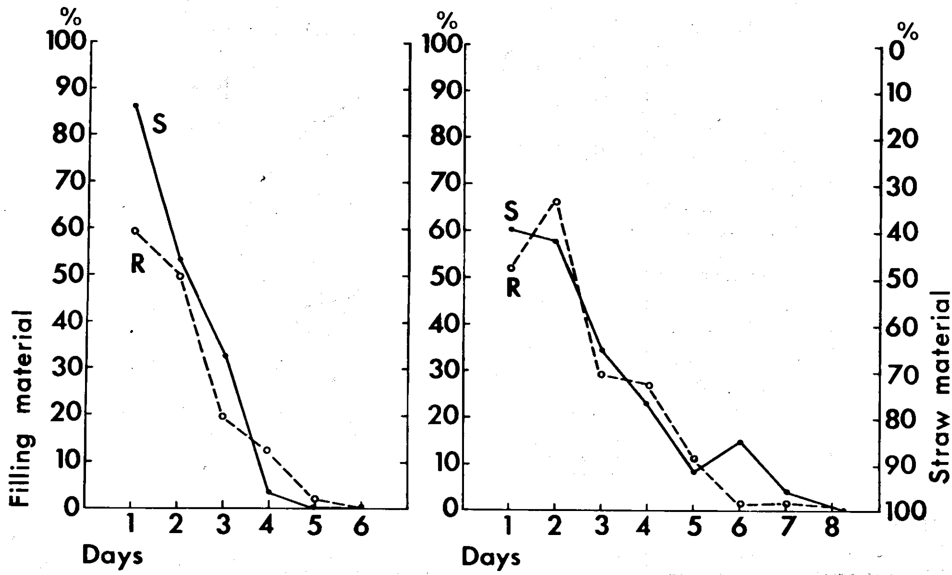


FIG. 11. Relative amounts of packing and fibrous material in standard nests (S) and nests in boxes of reduced cross-section (R). --- = reduced cross-section, ——— = standard nests. The number of nests upon which the averages are based is given in the figure.

10. A female with a very incomplete nest, which was given a very complete one (No. 7, Table 9), or vice versa (Nos. 9, 10, Table 9), deserted its nests. If the difference between the original nest and the exchange nest was smaller, the female accepted the strange nest, and continued to build.

On receiving a relatively complete nest, a female which has built only little seems to adjust herself to the new situation i.e. builds little (Nos. 1, 2, 3, 5, Table 10). The mean weight of nest material carried in by females which were given more complete exchange nests, amounted to only 12.77 g. This should be compared with the mean weight of standard nests, 22.2 g. On

TABLE 9. Exchange of nests: duration of nest-building. All figures given are days.

Nest No.	Original nest (a)	Exchange nest (b)	Built after exchange (c)	Time a + c	Time b + c
1	0+	4	3	3	7
2	0+	3	4	4	7
3	1	4	5	6	9
4	2	4	6	8	10
5	3	5	1	4	6
6	3	7	5	8	12
7	1	9	—	—	—
Mean			4.0	5.5	8.5
8	6	2	5	11	7
9	4	1	—	—	—
10	5	1	—	—	—

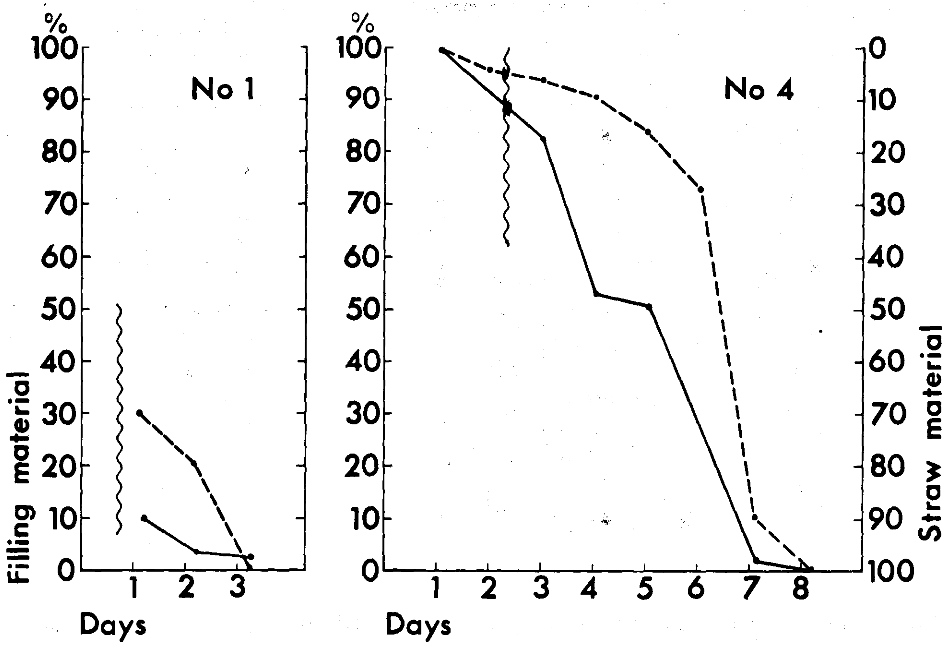


FIG. 12. Relative amounts of packing and fibrous material brought to nest-boxes in which the original nest was exchanged for a more complete one. { = introduction of more complete nest. Nest No. 1 was hardly started when the new nest was introduced, nest No. 4 was built during 2 days. The numbering of the nests is the same as in tables 9 and 10. - - - = weight, ——— = numbers.

the other hand, one female (No. 4, Table 10) which had built a half-complete nest before receiving a more complete exchange nest, went on bringing in material, corresponding to another half nest. Combined with the large amount of material in the exchange nest, this made an abnormally large nest.

The kind of material brought in by the females in the exchange experiments is exemplified in Figures 12—16. Females which had recently started to build

TABLE 10. Exchange of nests; weight of nests in g.

Nest No.	a Original nest	b Exchange nest	c Built after exchange	a + c Totally built by female	b + c Total weight of nest
1	0	23.89	4.08	4.08	27.97
2	0	14.99	5.16	5.16	20.15
3	0.87	15.30	7.94	8.81	23.24
4	11.41	31.48	13.19	24.60	44.67
5	14.99	29.11	1.22	16.21	30.33
6	16.48	?	1.28	17.76	?
Mean				12.77	29.27
8	29.11	15.66	0.67	29.78	16.33

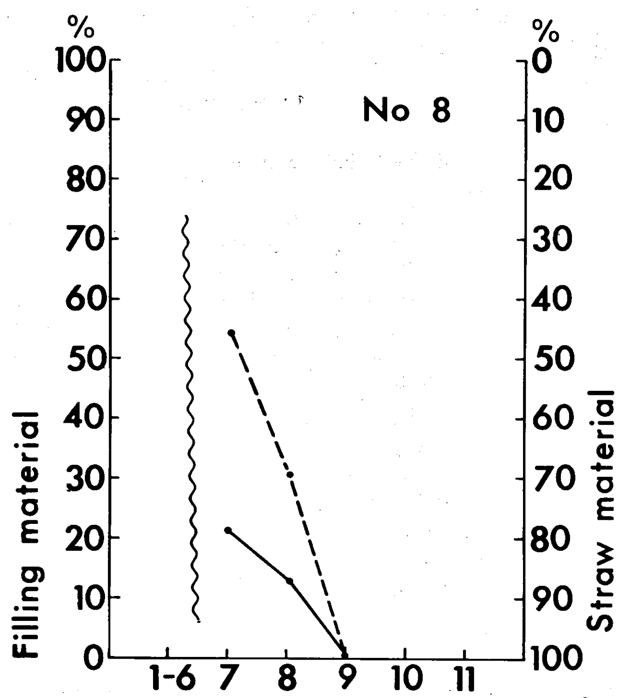


FIG. 13. Relative amounts of packing and fibrous material brought to a nest-box in which the original nest was exchanged for a less complete one { = introduction of less complete nest. Building had been in progress for 6 days when the exchange took place. The numbering of the nests is the same as in tables 9 and 10. --- = weight, ——— = numbers, x-axis = time in days.

and were given well-built nests adjusted themselves more or less to the new situation adding mainly fibrous material to the nest (nest No. 1. Figs. 12, 14, 16). But one female which had built her own nest for a longer period seemed

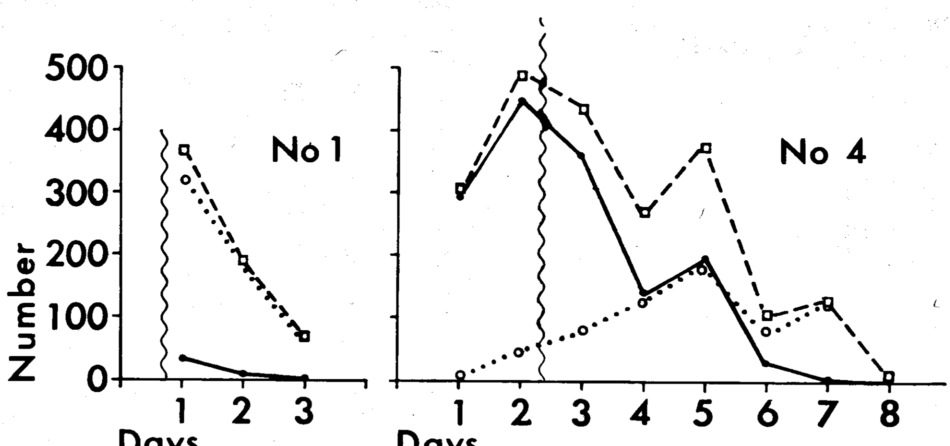


FIG. 14. Numbers of items of packing and fibrous material brought to nest-boxes in which the original nest was exchanged for a more complete one. } = introduction of more complete nest. Nest No. 1 was hardly started when the new nest was introduced, nest No. 4 had been under construction for 2 days. The numbering of the nests is the same as in tables 9 and 10. ——— = packing material, · · · · = fibrous material, - - - = total material.

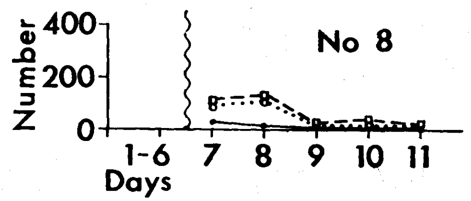


FIG. 15. Number of items of packing and fibrous material brought to a nest-box in which the original nest was exchanged for a less complete one. ⌇ = introduction of less complete nest. The nest had been under construction for 6 days when the exchange took place. The numbering of the nests is the same as in tables 9 and 10. ——— = packing material, ···· = fibrous material, --- = total material.

not to adjust on receiving the exchange nest, but went on bringing packing material to the nearly complete exchange nest (nest No. 4, Figs. 12. 14, 16). A female which received a less complete nest (nest No. 8, Figs. 13 and 15) used little packing material, but went on bringing fibrous material in small amounts to the incomplete nest. This female showed little adjustment to the new situation.

CURIO (1959) observed that a female Pied Flycatcher from whose nest he removed the inner layer, moved to another nest-box, and took over an old Pied Flycatcher's nest in this box, only adding an internal layer to the nest.

d. Nests built over nests of the Great Tit

This situation offers a natural experiment closely related to the exchange experiment just described. At the very start of nest-building, the female Pied Flycatcher is provided with a nest that is more complete, although very dissimilar to its own.

In all, three nests of the Pied Flycatcher were built over nests of Great Tits. The weights and building periods of these nests are shown in Table 11.

In two of these nests (a, b) the weight of the Pied Flycatcher's nest was quite typical (21.20 and 21.02 g against 22.2 g on an average in standard nests). In the third nest (c) the tit's nest seems to have inhibited the flycatcher's use of packing material, and this nest weighed only 8.72 g.

In nests a and b, the ratio of packing to fibrous material carried into the nest daily was similar to that in the standard nests. In nest c the existence of the

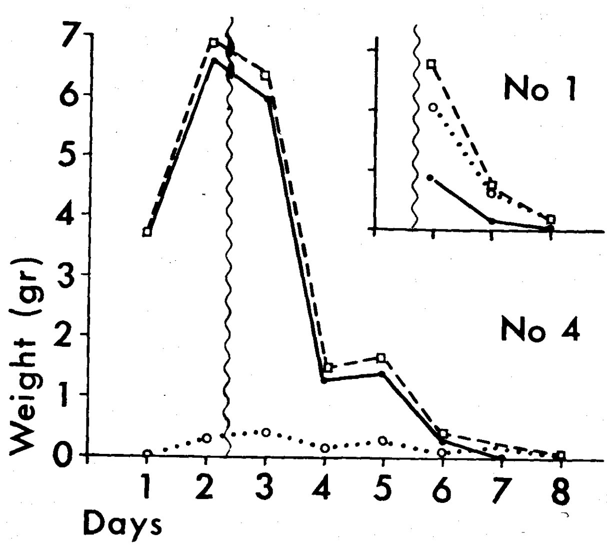


FIG. 16. Weight of packing and fibrous material brought daily to two nest-boxes, in which the original nest was exchanged for a more complete one. ⌇ = introduction of more complete nest. Nest No. 1 was hardly started when the new nest was introduced, nest No. 4 had been under construction for 2 days. The numbering of the nests is the same as in Tables 9 and 10. ——— = packing material, --- = fibrous material, --- = total material.

TABLE 11. Weights (in g) of nests of the Pied Flycatcher built over nests of the Great Tit.

	Nest a	Nest b	Nest c
Great Tit, nest weight	8.08	8.08	11.20
Pied Flycatcher, nest weight	21.20	21.02	8.72
Total weight	29.28	29.10	19.92
Building period, days	9	5	7

tit's nest obviously caused a reduction in the number and weight of the packing items (Figs. 17—19).

Without further studies, it is impossible to decide why two of the females reacted differently from the third.

IV. Summary and discussion

The Pied Flycatcher builds its nest of two types of material and with a restricted repertoire of fixed movements of feet, bill, wings, and breast. Almost identical movements are characteristic of other passerine birds with open, bowl-shaped nests, such as the Goldcrest (PALMGREN 1934), Chaffinch and Icterine Warbler (VAN DOBBEN 1949), Red-backed Shrike (KRAMER 1950), Lesser Whitethroat, Black-capped Warbler, and Icterine Warbler (DECKERT 1955), Great Reed-Warbler (KLUYVER 1955), Chaffinch (MARLER 1956), and Blackbird (LÖHRL 1972). The Starling, which builds a very simple nest, has a strikingly reduced set of building movements (DECKERT 1970). (For further comparative aspects. cf. DECKERT 1968.)

In the early stages of nest-building, the Pied Flycatcher brings more packing material than fibres to the nest, and a rough outer layer is formed. As nest-

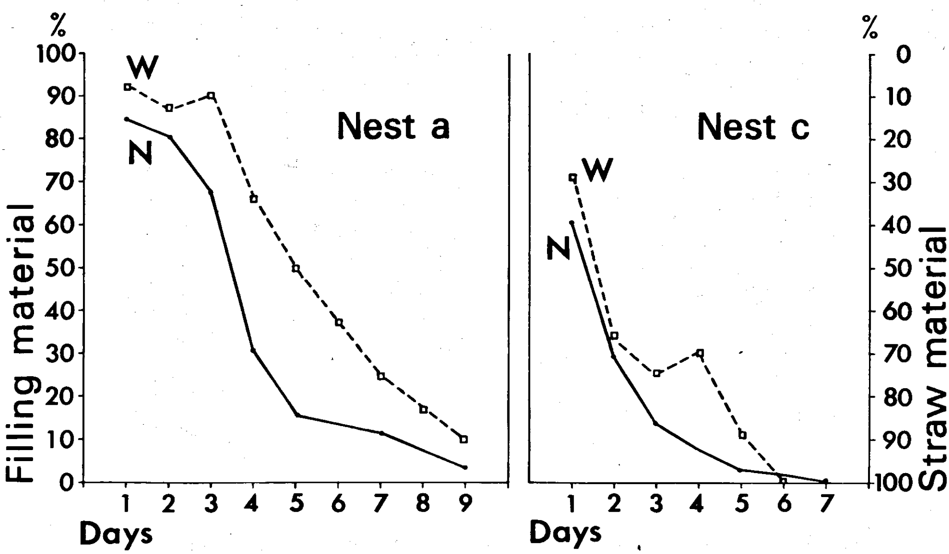


FIG. 17. Ratio of packing to fibrous material in nests of the Pied Flycatcher built over nests of the Great Tit. --- = weight, ——— = numbers. Nests a and c are the same nests as in Table 11. In nest a the female built independently of the tit's nest, in nest c the female, from the very beginning of nest-building, reduced the amount of filling material carried in.

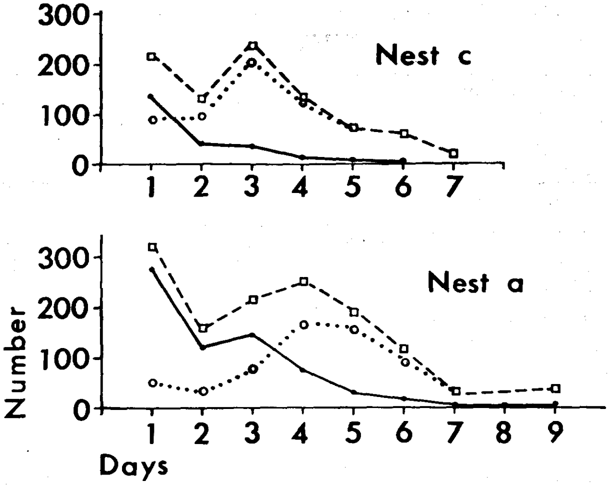


FIG. 18. Number of items of packing and fibrous material brought daily into two nests of the Pied Flycatcher built over nests of the Great Tit. ——— = packing material, · · · · = fibrous material, - - - = total material. Nests a and c are the same nests as in Table 11.

building progresses, the preference for fibrous material increases, finally reaching 100 per cent. The frequency of nest-building movements changes, and the female spends far mor time in the nest at each visit. In this manner an inner layer composed mainly of fibres is formed. The actual lining of the nest-bowl is composed almost entirely of very fine fibrous material.

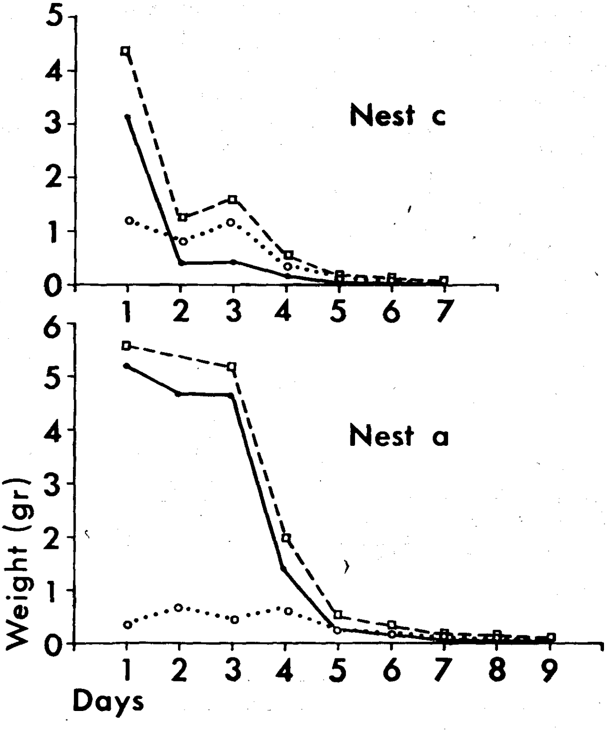


FIG. 19. Weight of material brought daily into two nests of the Pied Flycatcher built over nests of the Great Tit. ——— = packing material, · · · · = fibrous material, - - - = total material. Nests a and c are the same nests as in Table 11.

Theoretically, the different phases of nest-building may be released by either stimuli from the nest or internal factors in the female, or both. By modifying the external stimulus situation in three sets of experiments (i.e. (1) removing the nest-material daily, (2) providing narrower nest-boxes, (3) exchanging partly built nests for less or more completed nests) an attempt was made to clarify the relative importance of external and internal factors. The last-mentioned set of experiments was supplemented by a natural one, (4) Pied Flycatchers building over nests of Great Tits.

THORPE (1963) pointed out that if a bird is to produce a nest, it requires not only a set of fixed motor patterns, but also a mechanism for their coordination, created through a system whereby the releasing mechanisms of the motor patterns are exposed, at the right times, to adequate releasing or inhibiting stimuli. In the present study the existence of such external key stimuli emanating from the nest was confirmed in every experiment. The daily removal of nest material provides an example. The outer nest-layer never became complete, and therefore the female never passed into the phase of building the inner layer. But even so, internal factors seemed to play some role. The female did not, under these circumstances, go on building indefinitely, but eventually either deserted or laid her eggs in a very incomplete nest. Phenomena like an abrupt decrease of building activity the day before the commencement of laying (Figs. 8, 9) also testify to the existence of internal factors.

The experiments with narrower nest-boxes showed that the bird's choice of nest material is influenced not only by stimuli from the nest, but also by those from the nest-hole.

The exchange experiments, and the cases in which Pied Flycatchers built over the nests of Great Tits, showed that the flycatcher does not have to go through a fixed amount of nest-building to complete its nest, but can reduce its normal building activity considerably. However, in these experiments, the effect of internal factors was clear. For instance, only one out of three Pied Flycatchers building over a tit's nest produced a nest of reduced size.

VAN DOBBEN (1949) assumes that in the Icterine Warbler each successive stage of nest-building provides stimuli releasing the choice of nest material appropriate for the next stage. For instance, when, as a consequence of the increased height of the nest rim, the bird, scratching backwards with its legs, does not reach the bottom of the nest-bowl, it ceases to bring cobwebs to the nest. Again, when the nest-bowl fits precisely to its body, the bird ceases to carry in vegetable fibres and turns to horsehair to line the nest.

The experimental study by COLLIAS and COLLIAS (1962) on a weaverbird demonstrated convincingly that in this species every step of nest-building provides the stimuli necessary to release the next step. COLLIAS and COLLIAS demonstrated the existence of a considerable number of such steps or phases of nest-building and analysed the stimuli releasing the advance to the next phase.

In Canaries (HINDE 1958 cf. also HINDE 1967, HINDE & STEEL 1972, STEEL & HINDE 1972 a, b, WARREN & HINDE 1961) the shift from collecting fibres for the outer layer of the nest to collecting feathers for the inner layer is determined partly by an internal, probably hormonal, change in the female, partly by stimuli from the nest. Injections of oestrogen speed up both phases of nest-building. The transition from building with fibres to building with feathers correlates with increased sensitivity to tactile stimuli in the incubation patch (see e.g. HINDE 1967, STEEL & HINDE 1972 a). A similar correlation may exist in the female Pied Flycatcher, which towards the end of the nest-building period ceases to bring in packing material. The development and tactile sensitivity of the incubation patch is regulated hormonally (HINDE 1967) by the interplay of oestrogen and progesterone. Here, again, the presence of the male (WARREN & HINDE 1961) plays a role, as courtship is known to influence the production of oestrogen. VON HAARTMAN (1956 a) has shown that the start of egg-laying in the Pied Flycatcher is influenced not only by the temperature, but also by the time of arrival of the birds, which implies that early courtship leads to early laying.

Acknowledgements

I wish to express my gratitude to Prof. Lars v. Haartman for his aid in planning the work.

Selostus: **Kirjoseipon pesänrakennustekniikka.**

Naaraskirjosieppo rakentaa pesänsä kahdenlaisesta aineksesta. Rakennustekniikassa on erotettavissa rajoitettu määrä kiinteitä liikemalleja. Alkuvaiheessa se tuo pesään enemmän karkeaa kolon täyteainesta kuin hienompaa vuorausainesta, jolloin muodostuu pesän karkea ulkokerros. Rakentamisen edistyessä hienomman vuorausaineksen osuus lisääntyy ollen lopuksi 100 % (kuvat 1, 3 ja 4). Pesänrakennusliikkeiden frekvenssit muuttuvat (kuva 5) ja naaras viettää yhä enemmän aikaansa pesässä. Näin muodostuu lopulta pesän sisäkerros hienommista jouhimaisista aineksista. Pesänrakennuksen ei vaiheitten laukaisijoina toimivat joko sisäiset tai ulkoiset, pesän hetkellisestä rakennusvaiheesta peräisin olevat, ärsykkeet tai molemmat yhdessä.

Ulkoista ärsykeympäristöä muutettiin kolmessa koesarjassa: (1) poistamalla kaikki pesäkoloon kannettu rakennusaines päivittäin (kuvat 7—9), (2) tarjoamalla linnuille normaalia ahtaampia pönttöjä (kuva 11, taulukko 8), ja (3) vaihtamalla rakennusvaiheessa oleva pesä sitä enemmän (kuvat 12, 14 ja 16) tai sitä vähemmän (kuvat 13 ja 15) rakennettuun pesään. Näillä kokeilla yritettiin selvittää sisäisten ja ulkoisten tekijöiden osuutta pesänrakennuskäyttäytymisen säätelyssä. (3)-koesarjan kanssa samaa tyyppiä on luonnontilassakin tapahtuva "koe" so. tilanne, jossa (4) kirjosieppo rakentaa pesänsä talitiaisen pesän päälle (kuvat 17, 18, 19, taulukko 11).

Kaikissa koesarjoissa tuli selvästi ilmi, että ulkoiset ärsykkeet säätelevät kirjosiepponaaraan pesänrakennuskäyttäytymistä sekä kiinteiden liikemallien esiintymisen että rakennusaineen valinnan osalta. Kuitenkin sisäisilläkin tekijöillä on merkitystä, mitä osoitti mm. se, että koesarjassa (1) pesänrakennus ei jatkunut loputtomiin. Myös pesänrakennusaktiviteetin jyrkkä lasku juuri ennen munintaa osoittaa tätä (ks. kuvat 8 ja 9). Vaihtokokeet (3) ja tapaukset, joissa kirjosieppo rakensi pesänsä talitiaisen pesän päälle osoittivat, että kirjosiepon ei tarvitse käydä läpi vakiomäärää pesänrakennusta, vaan se voi vähentää normaalia työmääräänsä huomattavasti. Näissäkin kokeissa sisäisen säätelyn vaikutus oli selvä, kuten silloin kun kirjosieppo, joka rakensi pesänsä talitiaisen pesän päälle, ei merkittävästi vähentänyt työmääräänsä (taulukko 11, pesät a ja b).

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Received March 1974