

## The incubation rhythm of the female Pied Flycatcher (*Ficedula hypoleuca*) in the presence and absence of the male.

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In an earlier paper (v. HAARTMAN 1956 b), the influence of temperature on the incubation rhythm of the female Pied Flycatcher was discussed. In the present paper, the influence of the male is dealt with. Both studies show that the alternation of attentiveness and inattentiveness (KENDEIGH) of the incubating female does not wholly depend on an autonomous rhythm in her central nervous system, but is strongly influenced by external factors.

Before going into the problem, I wish to recall the following facts. In this species, only the female incubates. Many females are eagerly fed by their mates, but others have to get on unaided. Polygamy is not infrequent (v. HAARTMAN 1951), and most males leave their females when egg-laying starts, or even shortly before this (v. HAARTMAN 1951, 1956), to search for a new territory. If a male succeeds in getting a new female in his new territory, he will similarly abandon her, returning to his first mate. Also, if he does not obtain a new mate in the second territory, he will sooner or later leave it, and return. The second mate of a polygynous male often has to feed herself entirely during incubation.

### A comparison between different females.

With my students, I made a whole day study of two pairs of the Pied Flycatcher at the Zoological Station of Tvärminne on 13. 6. 1957 (Pairs A and B, cf. Fig. 1).<sup>\*</sup> Fig. 1 also includes observations on a pair C at Lemsjöholm on 21. 6. 1957. This pair was studied only during 11 hours 50 minutes. For those hours in which I spent only part of the time at the nest, the feeding frequency and incubation time were calculated by rule of three.

Most feedings occur inside the nest-box. Fig. 1 also shows feedings observed outside the nest-box. Of course, only some of these were

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<sup>\*</sup>The observations on Pair B contain a gap, the observer having missed the first time at which the female left the nest.

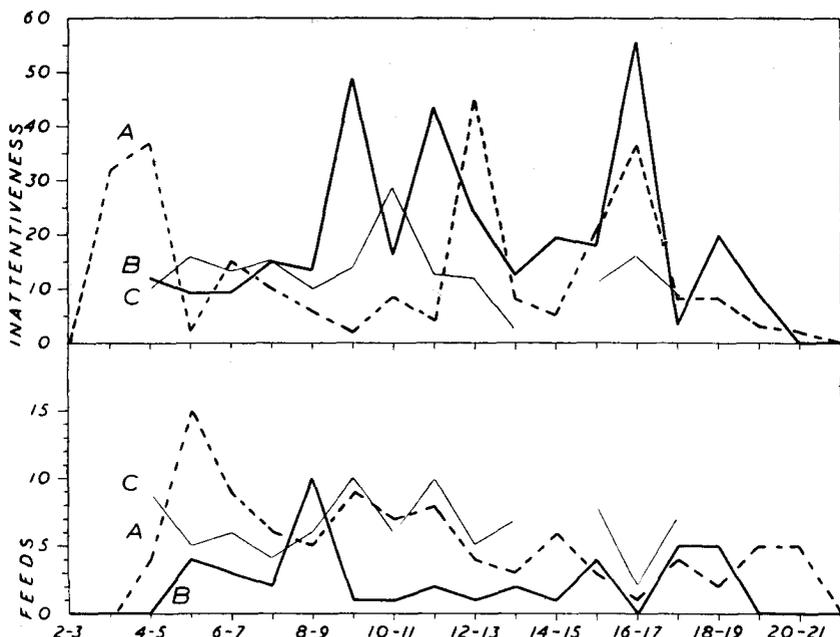


Fig. 1. Inattentiveness (in minutes per hour) in three different female Pied Flycatchers (above). Feeding frequency of the corresponding males (below).

observed, though the number of feedings missed was probably not very large.

There seems to be a clear correlation between the time spent on the nest by the female, and the feeding frequency of the male. In Pairs A and C the male fed eagerly, the female being as a rule less than 15 minutes per hour off the nest. The male B fed less frequently, the female spending more time outside the nest. (Cf. also table 2.)

It is theoretically possible that the low feeding frequency of the male B was a consequence of, not a cause of, the reduced incubation of the female. Every female may have her own rhythm, and the female B might have tended to incubate less than the females A and C. Such an objection can be refuted only if the behaviour of one and the same female with and without a mate is studied.

#### An experiment.

A pair (C) at Lemsjöholm was chosen as the object of study. The female laid the last egg on 11. 6. 1957. Incubation was studied on

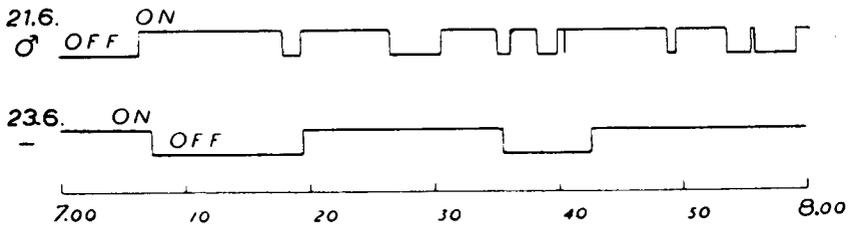


Fig. 2. A female Pied Flycatcher's periods on and off the nest in the presence (21. 6.) and absence (23. 6.) of the male. The period 7—8 a.m. was chosen as a sample.

21. 6. when the male was present. Then (22. 6.) I caught the male and transported him 30 km southwards. From earlier experience I knew that he would hardly return before 1958. On 23. 6. the incubation of the female was studied anew.

The temperature on both days was about the same (21. 6. during the observation period averaged  $+ 11.8^{\circ}$ , 23.6.  $+ 12.1^{\circ}$ ). On 21.6., I stayed at the nest between the following times: 4:00—9.30 a.m., 10.30 a.m.—1.48 p.m., 2.48—6.00 p.m., and at 23.6. on 4.02—9.02 a.m., 11.05 a.m.—1.45 p.m., 3.45—6.00 p.m. The observations on 23.6. were shorter because of heavy rain, which interrupted them. The bad weather on 23.6. cannot, however, be held responsible for the changed incubation rhythm of the female, as the change had already taken place before the first shower, at 9 a.m. (cf. Fig. 2).

Table 1 (cf. also Fig. 2) shows that the periods both on and off the nest were shorter when the male was present. The difference is larger with the periods off the nest. On 21. 6., when the male was present, the female only exceptionally remained more than 5 minutes away from the nest; periods of less than 1 minute occurred frequently. Hence the total time spent on the nest was much longer on 21. 6. (cf. table 2).

On 21. 6. the female was often induced by her mate to leave the nest. Out of 62 times when she left the nest, at least 26 were apparently caused by the appearance of the male. Often she left after having been fed, in other cases she heard the male outside, and joined him, begging for food. The rapid alternation between attentiveness and inattentiveness displayed by the female C is hardly typical of the species.

Table 1. Incubation rhythm of the female Pied Flycatcher C in the presence and the absence of the male.

Length of period	Periods on the nest		Periods off the nest	
	21.6. ♂ present	23.6. ♂ not present	21.6. ♂ present	23.6. ♂ not present
0—5 min.	18*	—	57	5
5—10	22	6	4	5
10—15	10	3	—	7
15—20	5	5	—	1
20—25	2	5	—	—
25—30	2	—	—	—
30—35	—	—	—	—
35—40	—	—	—	—
40—45	1	1	—	—
45—50	—	—	—	—
50—55	—	—	—	—
55—60	—	—	—	—
60—65	—	—	—	—
65—70	—	—	—	1**
No. of periods	60	20	61	21
Mean	9'20"	15'15"	2'30"	11'00***

Table 2 shows the amount of attentiveness in a number of incubating females. Females fed by their mates spent 70—80 % of the time incubating, whereas the female C spent only 58 % of the time on the nest after losing her mate.

Table 2. Attentiveness of some female Pied Flycatchers in relation to the feeding frequency of their mates. The pairs »1949» and »1955» were studied at Lemsjöholm. The pair »1955» is identical with the pair described by. v. HAARTMAN (1956) on 24. 6. 1955. The other pairs (A, B, and C) are mentioned in the text. Italics: calculated values.

Pair	♂ present or not present (+) (—)		♀ on the nest	♀ off the nest	Daily number of feeds given by the ♂
	present (+)	not present (—)			
C 21. 6.	+	—	9 h 16 min. (78.8 %)	2 h 30 min. (21.2 %)	100
A	+	—	12 h 30 min. (74.5 %)	4 h 16 min. (25.5 %)	96
1949	+	—	8 h 32 min. (76.4 %)	2 h 38 min. (23.6 %)	46
B	+	—	10 h 35 min. (70.4 %)	4 h 28 min. (29.6 %)	41
1955	+	—	8 h 25 min. (70.0 %)	4 h 28 min. (30.0 %)	?
C 23. 6.	—	—	5 h 33 min. (58.0 %)	2 h 30 min. (42.0 %)	—

\* 7 times of flying out and returning to the nest immediately are not included.

\*\* This period (65'45") was not a full one; the female was still off the nest when I had to leave.

\*\*\* Omitting the long period of inattentiveness (65'45"), the average period length was 8' 20".

That the presence of the male influences the attentiveness of the female indicates that his feeding plays a real part in her nutrition (cf. also v. HAARTMAN 1954), and that a female without a mate has to stay off the nest for a longer time, searching for the necessary food. A nestling Pied Flycatcher receives on average 4 to 6 feeds per hour, depending on the brood size, the corresponding values for the female being 2.75 (female B, table 2) to 6 (female C, 21. 6.). This does not mean that the female gets exactly the same amount of food, as the young receive on average 2.4 food items (v. HAARTMAN 1954) per feed, whereas I have the impression (from seeing many feeds inside the nest box with the »nidoscope», v. HAARTMAN 1952) that the female mostly receives only one. On the other hand, the number of observed feeds received by the female is a minimum number (especially in the female »1949», table 2, the number of feeds may have been considerably higher than observed). All the females I have studied so far caught a certain amount of food for themselves.

The weight of female C was 16 gm. on 21. 6. (male present), 15.5 gm. on 22. 6. (male caught 1 1/2 hours earlier), and only 14.2 gm. on 23. 6. (male caught more than 24 hours earlier; the day was rainy). All weights were taken between 6 and 7.30 p.m. Further investigations are needed to show whether incubating females without mates as a rule weigh less than other females.

#### Summary.

1. A whole-day observation of two pairs of the Pied Flycatcher (A and B) showed that the female A spent more time on the nest, the male A feeding more frequently.

2. The incubation of a female (C) was studied before and after the catching of her mate. The periods both on and off the nest were prolonged after the capture of the male, the latter, however, more so. The total amount of incubation decreased from about 79 % to 58 %. The weight of the female decreased from 16.0 to 14.2 gm. These findings confirm that the food given by the male is of real importance in the nutrition of the female during the incubation period.

**Literature:** v. HAARTMAN, L., 1951, Successive Polygamy. Behaviour 3: 256—274. — 1952, Svartvita flugsnapparens (*Muscicapa hypoleuca*) reaktion på sina ägg. Svensk Faunistisk Revy: 84—92. — 1954, Der Trauerfliegenschnäpper. III. Die Nahrungsbiologie. Acta Zool. Fenn. 83. — 1956 a, Territory in the Pied-

Flycatcher, *Muscicapa hypoleuca*. *Ibis* 98: 460—475. — 1956 b, Der Einfluss der Temperatur auf den Brutrhythmus experimentell nachgewiesen. *Ornis Fennica* 3, p. 100—107. — KENDEIGH, S. Ch., 1952, Parental Care and Its Evolution in Birds. *Illinois Biol. Monographs* 22: 1—358.

Selostus: 1. Tarkkailtaessa kahta kirjosiieppoparia (A ja B) vuorokauden ajan ilmeni, että naaras A käytti enemmän aikaa pesässä oloon kun taas koiras A ruokki useammin.

2. Erään naaraan (C) haudontaa tutkittiin ennen ja jälkeen kun koiras oli pyydystetty. Sekä pesässäolon että poissaolon kaudet pitenevät koiraan poistamisen jälkeen mutta poissaolokaudet pitenevät enemmän. Koko hautomisaika väheni 78 %:sta 58 %:iin. Naaraan paino väheni 16.0 g:sta 14.2 g:aan. Nämä tulokset osoittavat, että koiraan tuomalla ravinnolla on merkittävä osuus naaraan ravitsemuksessa haudonnan aikana.

## Tiaisparvista ja niiden liikunnoista.

LEO LEHTONEN

### Tutkimuspaikat, aineisto ja menetelmät.

Talvikauden parvilinnuista ovat Suomessa tyypillisimpiä havuja sekametsien tiaiset. Näiden — erikoisesti kuusitiaisen (*Parus ater*), tőyhtötiaisen (*P. cristatus*) ja hōmötiaisen (*P. atricapillus*) — toimintoja on kirjoittaja tutkinut vuodesta 1947 alkaen. Havaintojen keruu on tapahtunut pääasiassa Helsingin seuduilla, missä viisi metsikkōä on ollut pitkäaikaisten kontrollien alaisena. Nämä kaikki ovat olleet suurimmalta osalta mustikka- tai käenkaali-mustikkatyypisiä (MT-OMT), mutta niissä on ollut myös puolukkatyyppin (VT) laikkuja, kalliomännikkōjä ja pensaikkoja. Metsät sijaitsevat Kulosaarella, Laajasalossa, Munkkiniemi—Haagassa, Pasilassa ja Lauttasaarella. Nimenomaan vaelluksiin liittyviä seikkoja olen tutkinut sekä Korkeasaarella että Suomenlinnan Kustaanmiekassa. Helsingin seudun ohella olen vuodesta 1950 alkaen tehnyt järjestelmällisiä tiaishavaintoja Nastolan pitäjän Lankilan kylässä olevassa MT-OMT-VT metsikkōssä.

Parvielämän seuraaminen luonnossa on monessa suhteessa vaivaloista. On täysin mahdotonta pitää yhteisön kaikkia jäseniä — tai edes osaa — samanaikaisesti silmällä. Siksi olenkin pyrkinyt alusta pitäen kiinnittämään retkillä huomion joko parveen kokonaisu-