

Polygyny in the Pied Flycatcher *Ficedula hypoleuca* at Ammarnäs, Swedish Lapland

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The Pied Flycatcher males in the Ammarnäs area show lower frequency of polygyny (0-2 %) than has been reported from more central parts of the species range. During experimental conditions, however, which were supposed to favour polygyny, 9 % was reached. Thirty percent of the males showed polyterritorial behaviour, which is a lower incidence of polyterritoriality than reported from other studies. It is suggested that polygyny is infrequent as the females arrive early, the latest ones at the very start of the laying period of the population. The lack of "free" females may also reduce the inclination of males to show the polyterritorial behaviour; about one third of the territory holding males of the study area remained unmated.

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1. Introduction

The breeding biology of the Pied Flycatcher, in a nestbox population, has been under investigation in the Ammarnäs area since 1965 (Hanson et al. 1966). About 80 to 200 breeding pairs occupied the nestboxes in the different years (Nyholm & Myhrberg 1983).

The polygynous behaviour of the Pied Flycatcher has been the subject of several studies, and data concerning the frequency have been presented from several nestbox populations in different parts of the species' range. Thus, in Southern and central Scandinavia von Haartman (1951) observed that 7 % of the males were bigynous, and Askenmo (1977) and Lundberg et al. (1981) report this in 20-25 % and 10-35 % (of the breeding males) respectively. There were clear indications that the frequency of polygyny in every year, 1965 to 1979, was significantly lower in the Ammarnäs area at the northern margin of the species' range than in the studies referred to above. This was the incitement of the present study, which was undertaken in 1980, to examine the level of polygyny of the Pied Flycatcher in the Ammarnäs area and to suggest explanations for the low frequency of polygyny.

2. Material and methods

In one nestbox area ("E", 80 nestboxes, about 7 per ha) all males but 3 were colour ringed during the period of territory establishment so that the individuals could be recognized in the field. The identity of two of the unringed males was established by their characteristic song. The male's sites were carefully noted by daily observation, until the incubation phase was well advanced.

In the nestbox area "E" the number of nestboxes available for the Pied Flycatchers was doubled on June 1st, when corks were removed which initially closed the entrance hole of every second nestbox. This manipulation was expected to favour the possibility that the males would find suitable secondary territories to offer later arriving females, and so, to favour polygyny.

Unmated males and males which maintained a secondary territory were easily localized and identified, as they stood out distinctly by the high intensity of their song. In other nestbox areas, containing varied nestbox densities (4 to 7 per hectare), the relation: Male per active nest, was determined in the seventy-one nests in which young were hatched. The males were caught within the nestboxes, and ringed, when visiting to feed their young.

3. Results

3.1. Arrival in the breeding area

Males arrived from about May 18, and new males appeared not later than June 12 (Fig. 1).

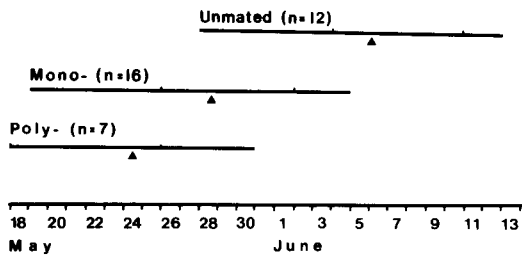


Fig. 1. Arrival dates of mono-, polyterritorial and unmated males in the nestbox group "E". — Triangle = mean date of arrival, vertical marks include period of 75 % male arrivals.

At June 1st territories containing about 75 % of the nestboxes were occupied, and nestbuilding was going on in about 65 % of the finally occupied nestboxes. Thirtyfive males finally settled in the nestbox area. Another two temporarily occupied territories in the area, but moved on. Females were first observed on May 23. Nestbuilding was started in the nestboxes from May 27 to June 10.

3.2. Maintenance of territories

Each territory generally included several nestboxes. When the female had decided where to breed, the male's interest to maintain the supernumary nestboxes in the territory diminished, and these could be taken over by later arriving males.

3.3. Monoterritoriality, polyterritoriality and polygyny

Regarding the territorial behaviour during the *laying period*, the males could be separated into two categories (Fig. 2). About 70 % (16 out of 23) of the males breeding in the nestbox area "E" remained faithful to the nest site (monoterritorial), where they showed low song activity. The other category, which comprised the remaining 30 % (7 out of 23 males) showed polyterritoriality and appeared with re-intensified song in a secondary territory. Two of the polyterritorial males were polygynous. The distances between the primary and the secondary nest were 40–180 m. In those seventy-one breedings in which young hatched in the other nestbox areas (see above), no case of polygyny was verified. Possibly, however, one of the clutches could have been a secondary clutch, as no male was observed

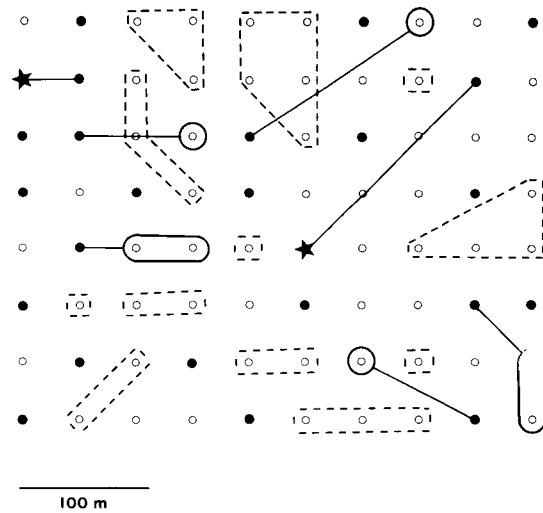


Fig. 2. The occupation of the nestbox group "E" on June 1st, showing the definite situation. — Solid circle = nestbox with nest. — Open circle = nestbox without nest. — Solid circle attached to open circles enclosed by solid lines = primary nest and secondary territory of polyterritorial male. — Solid circle attached to star = primary and secondary nest of polygynous male. — Open circle enclosed by broken lines = territory of unmated male.

to take part in the feeding of the young. The males' polyterritoriality was not studied in these cases.

3.4. Non-breeding, territory-holding males

Twelve (35 %) out of the totally 35 males which maintained territories in the nestbox area "E" remained unmated (Fig. 2). These males, average, arrived later in the area than did the breeding males (Fig. 1). Less than 20 % of those males which arrived after June 1st, and none after June 4th, became mated.

4. Discussion

Previous studies have shown that a high proportion of male Pied Flycatchers show polyterritorial behaviour. Thus von Haartman (1956) and Askenmo (1977) found that at least 65 % and 95 % of the males, respectively, were polyterritorial in nestbox areas in central and southern Scandinavia. Polyterritorial behaviour increases the fitness of the male if he becomes polygynous, (von Haartman 1969, Askenmo 1977, and Alatalo et al. 1981). This also seems valid for the

Table 1. Number of fledglings produced by mono- and polygynous Pied Flycatcher males at Ammarnäs. No. of males in parenthesis.

Year	Monogynous	Polygynous
1972	4.3 (14)	9.5 (2)
1973	2.9 (61)	10.0 (2)
1977	0.8 (13)	3.0 (1)
1978	1.7 (25)	9.0 (1)
1979	0.6 (30)	3.0 (1)
1980	4.5 (21)	9.5 (2)

Pied Flycatcher males in the Ammarnäs area (Table 1) and as in southern and central Scandinavia polyterritoriality should be to the male's advantage in this northern area.

The low frequency of polyterritorial males (30 % of the breeding males) which, however, occurred at Ammarnäs, indicates that the inclination of the males to exhibit polyterritorial behaviour can be modified by certain determinants. Lack of nestboxes for the establishment of secondary territories does not seem a probable limiting factor for polyterritoriality in the nestbox area "E", as the number of available nestboxes was doubled June 1st, a few days before the laying period of the population (Fig. 3). Further, most of the unmated males arrived during the later part of that period (Fig. 1), indicating that there were then still spaces for further territories to be established.

Low abundance, or lack, of late arriving females could be a factor limiting polyterritorial behaviour (and polygyny) in the Ammarnäs area.

The arrival dates of the females in the area were not thoroughly recorded, but that they arrived early relative to the laying period, and rather synchronously, was indicated by the fact that only 20 % and 0 % of the males which arrived later than June 1st and June 4th, respectively, got mated (Fig. 1). There was an obvious temporal relationship between the low abundance of "free" females which was indicated to occur after June 4th, and the low frequency of polyterritoriality shown by the males of those nests in which the first egg was laid after June 5th. Then, only 1 out of 11 males exhibited polyterritorial

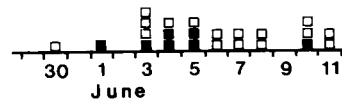


Fig. 3. Numbers of nests in which the first egg was laid, at different dates. — Open square = male monoterritorial. — Solid square = male polyterritorial.

behaviour, while 6 out of the 12 males of pairs breeding earlier did so (Fig. 3).

Cessation of female arrivals during the very first days of June might thus have limited the exhibition of polyterritorial behaviour. It would certainly mean that only a low frequency of polygyny would be possible, as, then the laying period had just begun. In only two nests did egg-laying occur before June 3rd (Fig. 3). The primary females of the two polygynous males started laying on June 4th.

The laying period of the year of this study was representative of the Ammarnäs area, as judged from the years 1965–1983. Only occasionally does laying start before June 1st.

Low numbers of late-arriving females which could be the ultimate factor limiting polygyny in the Pied Flycatcher in the Ammarnäs area, might be a typical feature in areas near the northern limit of the range of the species. It may be promoted by the high frequency of polyterritorial males in more southerly areas. The latest females to arrive were probably predominantly the youngest ones, which also have the weakest bonds to their sites of birth or first breeding. In the Ammarnäs area only about 16 % of the year X breeding females are potential returners to their breeding sites (Nyholm & Myhrberg 1983). Hence, young females may be preferentially attracted by polyterritorial males along the migratory route. Such a condition could also explain the superabundance of males in the Ammarnäs area, which was shown in the nestbox area "E" by the occurrence of 30 % more territorial males than breeding females.

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