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Brief reports

A case of polygyny in the Willow Tit *Parus montanus*

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Introduction

In 1987 I started a long-term project on the general biology of the Willow Tit *Parus montanus* in the birch alpine region in central Norway (Haftorn 1990). This species is considered to be strictly monogamous, and the pair bond usually persists until one of the mates dies (divorces occur rarely; Haftorn 1990). However, in 1989 I observed an extra-pair copulation (to be described elsewhere), and in the breeding season of 1992 I recorded an old male which simultaneously had two mates. To the best of my knowledge this is the first and only time that polygamy has been documented in this species.

Study area and methods

The study area is situated at Venabu (61°39′N 10°08′E) in the county of Ringebu, central Norway, about 900 m a.s.l. The forest consists mainly of birch *Betula pubescens*, intermingled with Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. Nearly all Willow Tits in the study area, that covers about 290 ha, were individually colour-ringed.

In the study area the Willow Tit raises only one brood a year. The clutch size is 6–11 eggs (mean ± SD = 8.1 ± 1.16, n = 37). The overall size of breeding territories is about 20 ha and the density of breeding pairs about 5 pairs/km^2.

The feeding rates of nestlings were recorded by direct observations at the nests. To get some information of the load size I video-recorded several feeding visits by the secondary female F2 during the last three days of the nestling period.

Detailed description of the event

Previous history

The particular male (M1) which turned out to be polygynous in 1992 was ringed as a an immigrant juvenile in August 1989. By then he had already joined the same winter flock as his future mate (F1), which at that time was paired with another male. When the latter male disappeared one month later (September 1989), the widowed female F1 re-mated with M1. This pair bred successfully in 1990 and 1991. In both years the male was almost certainly monogamous. During the winter of 1991–92 the old pair MlF1 was accompanied by two juveniles, forming a steady winter flock.

The 1992 scenario

On 30 May 1992 I discovered that M1 had got a new mate, viz. the yearling F2. Their nest (denoted B) in a rotten birch contained 7 slightly incubated eggs. At that time I assumed the old female F1 to be dead, but on 1 June she surprisingly turned up together with M1 at a feeder within his territory. Subsequently I found their nest with 8 eggs about 300 m apart from the other nest, also that one in a rotten birch. Only three eggs in the primary female's nest (denoted A) hatched, on 7 June. (The hatching success of this female was poor also in 1991; only 3–4 eggs of 8 hatched.) In the other nest (B) hatching took place 9–10 June (6 young, one unhatched egg). Thus, egg-laying started almost simultaneously in the two nests, although in nest A most likely 1–2 days ahead of the other. To equalize the number of young in the two nests, three nestlings from a third nest were transferred to nest A on 9 June and immediately adopted by the foster-parents (all young matched the same age). This was done in order to compare the abilities of the pair at nest A and the single-handed female at nest B to raise their offspring (see below).

The old male's secondary female F2 was ringed as a juvenile in an adjacent territory in October 1991. Together with two other juveniles she had by then joined an old male making a winter flock. She probably soon formed a pair with this old male (who had lost his previous mate in August 1991), but he disappeared before December 1991. Thereafter F2 associated with a juvenile male belonging to the same winter flock. This pair visited the mentioned feeder several times, but in spring 1992 the male disappeared (last observation 25 March). Shortly thereafter the assumed widowed female mated to M1, which she already knew from the many winter visits at "his" feeding table.

On 29 February I witnessed an aggressive encounter between female F2's mate at that time and her future polygamous mate M1. This skirmish took place at the border between the two territories, close to the site where the secondary female's nest was built later on. There was no evidence that the latter male expanded his territory notably after the assumed death of the other male. His secondary female nested within his territory anyway. Not until the beginning of June was the empty neighbouring territory occupied by a new male, viz. the intruder M2 (see below).

The breeding behaviour of the polygynous male (M1) — During the incubation periods, M1 visited both nests and fed the females, but his attentiveness was clearly biased towards the primary female F1. While she was fed 1.4 times per hour (observation time 341 min), the secondary female F2 got at best 0.5 feeds per hour (obs. time 629 min).

At 0758 on 9 June (hatching day in nest B) the secondary female solicited copulation with wing quivering and the precopulatory long-drawn *sisisi* call. The male M1 immediately responded by wing quivering and the same call while slowly approaching the female. At the moment of mounting he uttered a gargle. The copulation which took place on a dry birch branch 10 m from nest B, seemed to be complete. Once he was also observed copulating with the primary female, and noteworthy, only 30 m apart from the secondary female's nest. This happened at 1028 on 28 June, five days after fledging of the young in nest A.

As soon as the eggs hatched in nest A, the male started feeding the young. His mean feeding rate during the first four days was 6.9 visits per hour, compared to only 1.3 feeds by the female (obs. time 495 min). During the last three nestling days he still fed 6.6 times an hour, while the female's feeding rate had increased to 9.1 visits an hour (obs. time 145 min).

In contrast, the secondary female F2 did not get any help from the male to feed her nestlings. The first three days she fed 5.1 times per hour (obs. time 602 min), during the last three days 22.2 times an hour (obs. time 462 min) and during the previous six days 19.9 times on the average (obs. time 557 min). For comparison, the combined feeding visits of the male and the primary female at nest A was only 15.7 during the last three days. For this period the difference between nests was significant (Mann-Whitney U-test 2-tailed, $P = 0.04$).

There is no evidence that F2 brought smaller food-loads than F1 and the male to the nestlings. Video recordings show that F2 regularly brought large bundles of insects during her feeding visits, often consisting of several caterpillars in addition to a bunch of smaller arthropods.

Although the male entirely ignored the nestlings of his secondary female F2 he paid irregular visits to her nest. Several times he was also observed collecting caterpillars close by, but these were consistently brought to nest A. Occasionally, the male contacted F2 at her nest and the pair went foraging into the surrounding wood. After some minutes the female returned to nest with food, but never the male.

The young in nest A fledged on 23 June at the age of 17 days and were attended by both parents during a period of unknown length. Independent young were observed on 14 July, at which time they had already formed flocks with juveniles from other broods.

The young in nest B were at the point of leaving on 28 June and apparently did so the next morning at the age of 20–21 days. The fledglings were, at least partly, fed by the female until 14 July. The next day the family flock was still intact and even the male M1 paid a visit, although without offering food. The following day the young dispersed. Thus, the period of parental dependence lasted 17 days for these fledglings.

The primary female (F1) visiting the nest of the secondary female (F2) — While watching nest B on 27 June at 1214, I was surprised by the arrival of the primary female F1 from nest A. She went silently directly to the nest entrance, but stayed there only for a couple of seconds and did not enter the hole. Thirty minutes later she was back again, and for a third time 6 min thereafter. During a total observation time of 438 min on this and the following day, she visited nest B 13 times, i.e. 1.8 times per hour. She was completely silent and took invariably advantage of the absence of the secondary female. Neither was she guided by the male. She consistently spent only a few seconds at the nest, either clinging to the entrance or perching about one meter apart. Although her visits induced intense food begging by the nestlings she never brought food and did not even look into the nest.

Discussion

Polygamy has so far been documented only in a few species of the genus *Parus*. In a recent review Møller (1986) credited only the Blue Tit *Parus caeruleus*, in which polygyny occurs regularly at least in parts of Europe. Thus, in a Belgian population the estimated proportion of polygynous males was 3.4%. One male had simultaneously three females (Dhondt 1987a). Even a case of polyandry was proven (Kempenaers 1993).

In the Great Tit *P. major* only one European case of polygyny has been reported (Gooch 1935), but the evidence was questioned by Dhondt (1987b). In Japan, however, Saitou (1979) recorded several cases of bigamy and even trigamy in this species. von Haartman (1969) additionally included the Coal Tit *P. ater* among European polygynous species, referring to Nethersole-Thomson (1951). The latter gave no details, however. Thus, up to now polygamy has been firmly documented only in two European parids, viz. the Blue Tit and the Willow Tit.

In the American Black-capped Chickadee *P. atricapillus*, which is closely related to the Willow Tit, only two cases of polygamy have been reported so far (Smith 1967, Waterman et al. 1989), one of which concerned a female simultaneously mated to two males (polyandry). In the other case Smith (1991) suspected that the secondary female had lost her mate very early in the breeding season and that one of the neighbouring males simply had expanded his territory to include that of the widowed female. Interestingly, the present case of polygyny in the Willow Tit seems nearly identical to this scenario. The secondary Willow Tit female F2 in fact lost her previous mate early in the breeding season of 1992.

An unpaired male intruder (M2) showed a great "interest" in F2 who nested close to his territory although on Ml's side of the border. F2 alone provided all the food to the nestlings and did not get any help from her polygamous mate M1. Although M2 followed her tightly on her feeding visits to the nest, he neither took part in this business nor visited the nest. Clearly he had no relationship to the young. The female was never seen soliciting copulation to achieve "marriage entrapment" (sensu Gjershaug et al. 1989) and thereby encourage M2 to feed her young.

Like the polygynous Willow Tit, polygynous Blue Tits defended a single territory, but in contrast to the Willow Tit the male Blue Tits helped feeding the young of both broods (Dhondt 1987b). Although alone, the secondary Willow Tit female F2 successfully raised her brood of 6 young.

The nestling periods in F1 and F2's nests differed by 3–4 days. The longer period in F2's nest seems reasonable provided the young got less food than in the other nest. However, the single-handed female F2 fed the young at an even higher rate than F1 and the male combined and there is no evidence that she brought less food per feed either. The discrepancy of the nestling periods is therefore not easily explained.

The secondary female's former mate disappeared (probably died) late in March or beginning of May. The reason to polygyny in this case may therefore be as simple as lack of an unpaired mate. She mated to her close neighbour M1, which then became a bigamist. The feeder within Ml's territory (see above) was not in use during the critical mating period, so that it is unlikely that this feeder influenced her choice of sexual partner. Dhondt (1987b) concluded that the Belgian data on the mating systems of the Blue and Great Tits supported the polygyny-threshold model (Verner & Willson 1966). The present case of polygyny in the Willow Tit is not conclusive with respect to this model, although the model seems less likely because availability of appropriate food was probably of no constraint in any parts of the study area (a high density of caterpillars provided the bulk of the nestling food). The same applies to the deception hypothesis, proposed by Lundberg & Alatalo (1992) to explain polygyny in the polyterritorial Pied Flycatcher *Ficedula hypoleuca.* That the secondary female was deceived by male M1 into polygyny is improbable for two reasons. Firstly, both females nested within the same territory about 300 m apart. Secondly, female F2 had undoubtedly met M1 and his mate female F1 many times during the previous winter (at a feeder) and the spring, e.g. during territorial encounters, and therefore most likely was fully aware of his mating status. On the other hand, the frequent cryptic visits which the primary female paid to the secondary female's nest strongly indicate that she was well informed about her mate's bigamy.

Although polygamy was previously unknown in the Willow Tit it may be more common than hitherto believed. The polygynous male in the present case did not offer his secondary mate any help in feeding the young. If this is typical to the species, polygamous events are easily overlooked.

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