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Why are some Wood Warbler (Phylloscopus sibilatrix) males polyterritorial?

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Polyterritorial behaviour in male Wood Warblers (*Phylloscopus sibilatrix*) might occur either because 1) behaving as unpaired in a secondary territory will facilitate the attraction of a second female, and/or 2) the primary territories are not of sufficient quality to support two broods. Both these hypotheses build upon the assumption that vacant areas suitable for territory establishment are available. To determine the relevance of these hypotheses the polyterritorial behaviour of Wood Warbler males was studied in three different areas. The areas differed in quality (i.e. abundance of potential food). No differences were noted in polyterritorial behaviour in the different areas. An attempt was made to determine whether empty "potential territories" were available closer to the primary territory than the secondary. The results indicate that this was the case.

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1. Introduction

In passerines, both parents are often needed to rear the young successfully if the parents' reproductive success is to be maximized. When male assistance is not needed during egg-laying and brooding, the male has a chance to attract a second female. Why females are willing to mate with already-mated males has been explained by a number of female-choice models (Verner & Willson 1966, Orians 1969, Weatherhead & Robertson 1979). According to these models, access to a high quality territory or male could counterbalance the loss of full male-assistance.

When the male establishes two spatially separated territories, the female will find it difficult to know his marital status. In these cases female choice models are not applicable (Wittenberger 1976). Alatalo et al. (1981, 1982) suggested a "deception hypothesis" to explain polygyny in the polyterritorial Pied Flycatcher (*Ficedula hypoleuca*). To behave as unpaired in a secondary territory could give the female the false impression of an unpaired male and therefore increase his likelihood of attracting a second female. That it is a disadvantage to be a secondary female compared with primary females or females with monogamous males is clearly shown in the Pied Flycatcher data obtained by Alatalo et al. (1981, 1982).

Polygyny has been found to be quite common in some populations of Wood Warblers (*Phylloscopus sibilatrix*) (Fouarge 1968, Herman 1971, Ovchinnikova & Firsova 1971, Ovchinnikova 1973, Wesolowski 1980). In some cases the males are polyterritorial, but only as exceptions to a general monoterritorial behaviour in the populations.

Male Wood Warblers usually arrive at the breeding area before the females, but there is a considerable overlap (Fouarge 1968). The male sings intensively until paired, when singing activity decreases (Aschenbrenner 1966, Fouarge 1968, Temrin et al. 1984). After a few days he may take up singing again, but does so in a secondary territory (Temrin et al. 1984) or in an outlying part of the primary territory (Herman 1971; Wesolowski 1980).

The female takes sole care of nest-building and brooding the eggs (Fouarge 1968). When the eggs hatch, the male invariably stops singing elsewhere and helps feed the young. Low singing frequency and short song phrases are limited to the area around the female and the nest, while song flights, long song phrases and intensive singing occur in the "singing/display area" (Temrin et al. 1984).

In a study of the Wood Warbler in central Sweden (Temrin et al. 1984) all paired males were polyterritorial and some of them succeeded

in attracting a second female. Why should all the males in this area have been polyterritorial? Possible explanations to explain polyterritoriality in the Wood Warbler were suggested by Temrin et al. (1984):

1. The attraction of a second female could be facilitated if the male gave the impression of being unpaired in a secondary territory.

2. The primary territories were not sufficient (in terms of quality) to support two broods.

Both these hypotheses build upon the assumption that vacant areas suitable for territory establishment ("potential territories") were available.

This study is an attempt to determine the relevance of these hypotheses.

2. Methods

The studies were carried out near to Nyköping in central Sweden, during the spring and summer of 1983. The birds were individually colour-marked with plastic rings. The males polyterritorial behaviour was studied in three different areas.

Area 1 consisted of approximately 50 ha of arable and pasture land with small pockets of deciduous wood, and coniferous forest with scattered deciduous trees. Area 2 (21 ha) consisted of coniferous forest with scattered deciduous trees. Area 3 was a geographically clearly defined island of mixed deciduous woodland surrounded by arable and pasture land. This area was 18 ha.

Three methods were used in an attempt to check the quality of the territories in the three areas. 1) To assess the amount of food available in the lower vegetation four samples were taken with a sweep-net (each of 30 sweeps) in randomly chosen territories in each area. The collected insects and spiders were classified roughly into families, the length of each animal was measured and their dry weight determined. The dry weight was used in the comparisons. 2) To assess the amount of food available in the higher vegetation insect faeces were passively collected for a total time of 72 h in four containers in each territory (Larsson & Tenow 1975). The dry weight of the collected sample was determined. 3) The vegetation was censused in 30 m squares in the territory. The measurements were made on the same time in the different areas. This was done the week before the nestlings fledged.

It is difficult to know exactly what Wood Warblers feed on. This should differ both depending on what is available in the area and the time of the season. The rough classification of the possible food items collected indicated that most of the sweep-net samples reflected what Wood Warblers are supposed to feed on, according to both own observations and other studies (see Aschenbrenner 1966 for a review).

If the reason for the polyterritorial behaviour was that the territories were not sufficient to support two broods, one could expect that birds in a "rich" area would not be polyterritorial. Habitat quality was measured using the three methods described above in two primary and two secondary territories in each of the three areas.

If empty "potential" territories were found close to the primary one, the distance to the secondary territory could not be explained by lack of adequate territories closer at hand. To see if there were empty "potential" territories closer to the primary ones than the secondary territories chosen, primary and secondary territories of four clearly polyterritorial males were compared with a potential territory close to the primary territory.

I will label males with a singing place more than 150 metres from the nest polyterritorial, and males with a singing place closer to the nest monoterritorial.

Some of the values from the statistical tests are not given in the results, because of the editor's objections.

3. Results

3.1. Differences between the three areas

The mean values for the individual territories in each area show that the two territories in Area 3 have higher values than the individual territories in the other two areas (Table 1). A one-factor ANOVA (Analysis of variance) showed that there were significant differences between the areas on the insect faeces and sweep-net samples measures. Neuman-Keuls multiple range tests were used to determine which pair-wise comparisons were significant. On both measures, Area 3 was significantly different from Area 1 and 2, while there was no significant difference between Areas 1 and 2.

The six individual primary territories were then tested against each other. A one-factor ANOVA showed that there were significant differences between the territories for insect faeces and sweep-net samples. Each of the territories in Area 3 were significantly better than the individual territories in areas 1 and 2 in terms of the insect faecal samples (Neuman-Keuls multiple range test). The same two territories were significantly better in three cases on the sweep-net samples, and in the other three cases the probability was less than 0.1 (Neuman-Keuls multiple range test). There was no difference bet-

Table 1. Mean values of "food richness" for individual territories and areas. Numbers are relative values proportional to dry weights of insects and spiders in "sweep-net samples" and collected faeces in "insect faeces".

Territories	Sweep-net sample	Insect faeces
Area 1	57	6
Male nr 12	59	7
Male nr 13	55	4
Area 2	60	2
Male nr 20	64	2
Male nr 21	57	1
Area 3	129	67
Male nr 3	132	63
Male nr 9	125	71

ween the individual territories in areas 1 and 2 ($P > 0.50$ in 11 out of 12 cases, and in one case > 0.10).

Four of the six males in the sample were clearly polyterritorial. Their primary and secondary territories were put together and tested in the same way as described above. The male in Area 3 had significantly better primary and secondary territories than the three males in the other two areas (Neuman-Keuls multiple range test). There was no significant difference between the males in areas 1 and 2.

The description of the vegetation in the territories show that the territories in Area 3 had higher frequencies of deciduous trees, and that the numbers of large trees were higher there than in areas 1 and 2. The most common deciduous tree species in the territories was birch. Hazel was also common in all the territories, while limetrees were fairly common in Area 3, but did not occur elsewhere. Spruce was the most common coniferous tree.

3.2. Were the males in the rich area less polyterritorial?

Area 1. Only three males stayed in the area. A few more were observed singing for some days, but later disappeared. Two of the three males were clearly polyterritorial, with secondary territories 225 and 350 m from their nests. The third male was frequently away from his primary territory, but a secondary territory could not be found. When his female started to brood the eggs he was observed singing intensively 75 m from the nest, where another male had been singing for a week before.

The male who had a secondary territory 225 m from his nest succeeded in attracting a second female when his first female was brooding the eggs. The second female was deserted when the first female's eggs hatched, and both parents fed the nestlings. The deserted second female successfully raised 6 young on her own.

Area 2. Five males held territories in this area. All were paired. Two of these were clearly polyterritorial and had secondary territories 250 and 550 m from their primary nests. The other three males had "singing places" about 50, 60 and 75 m from their nests.

Area 3. (The "rich" area.) Seven males held territories in this area. All were paired. Three males were polyterritorial, with secondary territories at distances of 165, 200 and 300 m from their nests. The other four males had "singing/display areas" 60, 65, 70 and 90 m from their nests.

When comparing the behaviour of the males in the three areas, no difference could be found in the rate of polyterritoriality or in their behaviour.

3.3. Were there empty "potential" territories close to the primary territories?

Four clearly polyterritorial males' territories were investigated. The primary, secondary and an empty "potential" territory close to the primary were used. A comparison (ANOVA) of the data from the insect faeces and sweep-net samples indicates that there are no significant differences between the four primary territories and either the "potential" or the secondary territories (Table 2).

If we look at the three territories for each male separately, the mean values are as good or even better for the "potential" territories than for both primary and secondary, which also indicate that other factors are important when Wood Warblers choose territory.

Two of the males (12 and 13) are from Area 1. Both these males' "potential" territories were approximately 60 m from their nests and were chosen as having been territories where Wood Warblers successfully bred the previous year. Male 13 had a secondary territory consisting mainly of coniferous trees that seemed to be poorer (sweep-net samples) than his "potential" territory, which consisted of only deciduous trees (Table 2).

4. Discussion

4.1. Differences between the three areas

Area 3 is known as a very good habitat for both warblers and insects. The results confirm the

Table 2. Mean values of "food richness" for three types of territories, (primary, secondary and potential) calculated as in Table 1.

Territories	Sweep-net sample			Insect faeces		
	Prim	Sec	Pot	Prim	Sec	Pot
Area 1						
Male nr 12	59	84	247	7	21	25
Male nr 13	55	32	85	4	5	5
Area 2						
Male nr 21	64	57	74	1	7	2
Area 3						
Male nr 9	125	100	115	71	141	24

expected difference between Area 3 on one hand and Area 1 and 2 on the other. The difference in "richness" did not seem to influence the male's behaviour. The males were just as polyterritorial in Area 3 as in the other two areas. The degree of polyterritoriality was not influenced by the "richness" of the territories.

One important question is whether the sweep-net samples and insect faecal samples really reflect the availability of food for the Wood Warbler. Although neither of the measures is entirely satisfactory, both concur in distinguishing Area 3 as being richer than Areas 1 and 2.

4.2. Primary, potential and secondary territories

One more difficult aim of this study was to determine whether there was an equally good empty area as the secondary territory closer to the primary territory. The results indicate that this might have been the case. It remains possible, of course, that real differences were masked in the data either because the sample size was not large enough or because the factors investigated are not the determining ones for the Wood Warbler when choosing territory. A strong indication that the males preferred to be at a large distance from the female/nest, although "potential" territories were closer at hand, was that two of the polyterritorial males in Area 1 had empty areas close to the primary territories that had successfully been used as primary ones the year before.

4.3. Why are some Wood Warbler males polyterritorial?

Female choice models predict that, when a female mates with an already-mated male, the demands for male or territory quality should be rather high. Polyterritoriality might be a way in which males escape this female-imposed constraint.

Female-female aggressiveness should not be an important reason for polyterritoriality in the Wood Warbler, since monoterritorial polygyny has been found to be rather common in some populations (e.g. Herman 1971). 40% of the males in a Polish population were polygynous (Wesolowski 1980); they were monoterritorial and density was so high (10 pair/10 ha) that there was no room to establish secondary territories (Wesolowski, personal communication). In central Sweden, rather close to the northern boundary of the Wood Warbler range, there seems to be a surplus of "potential" territories. In 1982, there were seven males holding territories in Area 1. Six of those were paired, and two of those were polygynous (Temrin et al. 1984). Only one of the primary and secondary territories used by the males in 1982 was used as primary territory in 1983. One other was used as a secondary territory.

The results of this study indicate that the reason for polyterritoriality among the studied males is not that the primary territory could not support two broods or that potential territories were not available close to the boundary of the primary territory. Instead the most likely reason is that when empty territories are available, the male could increase the likelihood of attracting a second female by behaving as though he was unpaired in a secondary territory.

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