ORNIS SCANDINAVICA 15: 63–66. Copenhagen 1984

Removal experiments in a population of Willow Warblers Phylloscopus trochilus in mountain birch forest, in Ammarnäs, Swedish Lapland

Björn Arvidsson and Per Klaesson

Arvidsson, B. and Klaesson, P. 1984. Removal experiments in a population of Willow Warblers *Phylloscopus trochilus* in mountain birch forest, in Ammarnäs, Swedish Lapland. – Ornis Scand. 15: 63–66.

In 1977 and 1978 respectively, 3 and 4 territorial Willow Warbler males were removed with mist-nets in a subalpine birch woodland in Ammarnäs, Swedish Lapland. Each year one new male established a territory in the vacated area. The surrounding males enlarged their territories slightly but not much enough to fill up all of the emptied area. In control areas no changes occurred. It is concluded that territorial behaviour of the stationary males exclude some males of the same species from establishing territories. The new males probably failed to get breeding partners and it is thereby possible that the reproductive output of the population was not affected by the exclusion of some males from breeding.

B. Arvidsson, Nylösegatan 11 C, S-415 03 Gothenburg, Sweden. P. Klaesson, Pl 1615, S-430 30 Frillesås, Sweden.

Introduction

Using removal experiments, it has often been shown that territoriality of stationary males excludes other conspecific males from taking a territory and breed (Watson and Jenkins 1968, Harris 1970, Zwickel 1972, Knapton and Krebs 1974, Wesolowski 1981). Such exclusion may also affect the average reproductive rate of a population with an equal sex ratio if some females at the same time are prevented from breeding (Brown 1969).

We made removal experiments with the Willow Warbler, a strictly territorial bird species, in subalpine birch woodland in Ammarnäs, Swedish Lapland. The two experiments, that were performed in 1977 and 1978, were a part of a larger investigation program on the breeding ecology of the Willow Warbler in mountain birch forest. In this habitat the dynamics of bird communities have been investigated since 1963 (the Luvre-project – see Enemar 1969, 1982). Thirtyfive to forty per cent of the bird community here consists of Willow Warblers (Enemar and Sjöstrand 1972).

Study areas and methods

The removal experiments were carried out on the southern slope of the mountain of Kaissats (68°58'N, 16°13'E), 7 km W of Ammarnäs in Swedish Lapland. The habitat is a representative part of the subalpine birch forest which has a mosaic pattern with wet and dry parts alternating. The dominating tree is the birch *Betula pubescens* with a medium height of 3–5 m. The scrub vegetation consists in dry areas of junipers *Juniperus communis* and in moist areas of willows *Salix* spp. The herb flora is rather luxuriant, especially in moist areas, with *Aconitum septentrionale* and *Lactuca alpina* as conspicuous plant species.

In 1977 a 24 ha area was used for the removal experiment. As a control area a smaller one nearby but down the slope was used. The habitat of the control area was more of heath type with fewer scrubs and shorter herb vegetation. In 1978 an enlarged area of 48 ha was used, including the area used in 1977. The western part of this area served as a control and the other part for the removal.

Accepted 15 August 1983

All males present in the areas were captured in mist-nets shortly after the arrival in the beginning of June. They were ringed with unique combinations of coloured plastic-rings that made individual recognition possible. Territories were accurately mapped using both spontaneous singing and singing induced by play-back technique. Mapping lasted about two weeks each year.

After the removal both the experiment area and the control area were under constant surveillance allowing new males to be detected immediately. About two weeks after the removal a new mapping was undertaken to reveal any changes that had occurred in the areas.

Results

In 1977 the removal was carried out 2 July and at this date the breeding population was at the end of the incubation period. For the removal 3 males in the centre of the area were chosen and captured in the mist-nets (Fig. 1). One day after the removal a new male appeared in the vacant area. The new male was very aggressive and reacted strongly on play back song. No female was observed together with this male at any time and it is probable that the new male never nested, maybe because of the late time in the breeding season. Some of the emptied space not occupied by the new male was divided among the surrounding territorial males (Fig. 2).

Mapping in the control area was not satisfactorily done but nothing indicated that new males established territories there. The situation was somewhat confused as some Willow Warbler pairs already had nestlings and silent males not previously ringed appeared in the control area searching for food.

In 1978 removal was performed on 25 June. The population was at this date in the middle of the incubation period. For the removal 4 males were chosen (Fig.

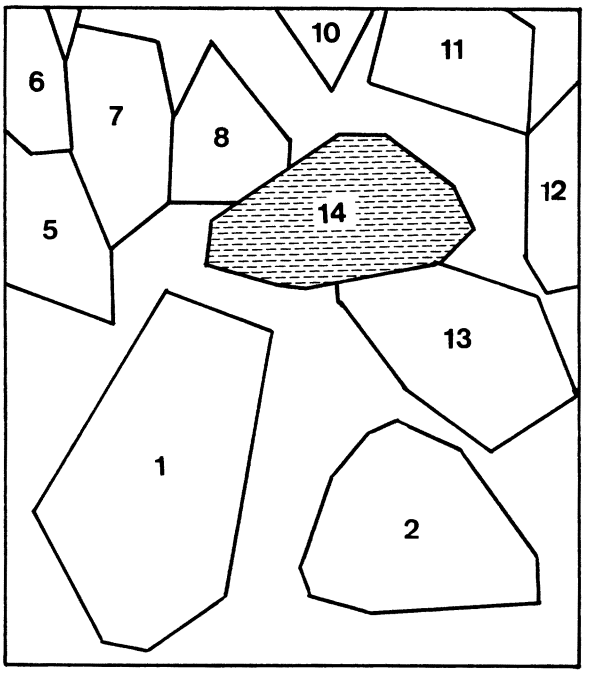

Fig. 2. Song-territories of Willow Warbler males after removal in 1977. Territories numbered as in Fig. 1. The territory of the new male (no. 14) shaded.

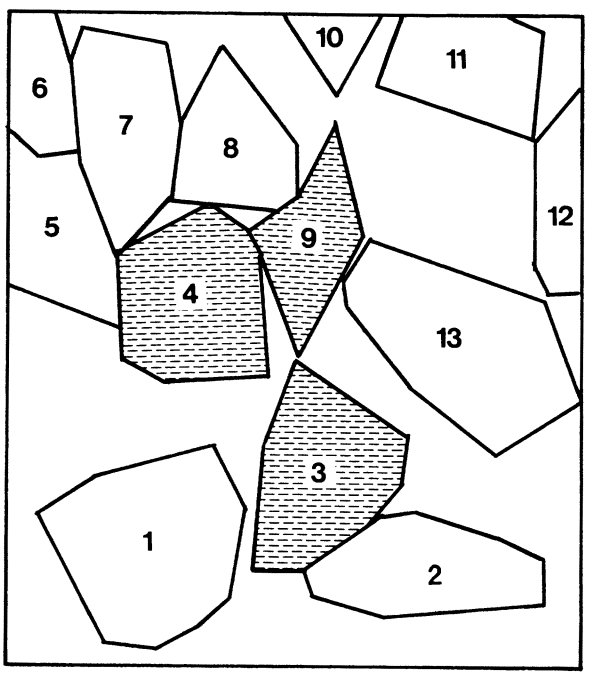

Fig. 1. Song-territories of Willow Warbler males before removal in 1977. Territories of removed males (no. 3, 4, 9) shaded.

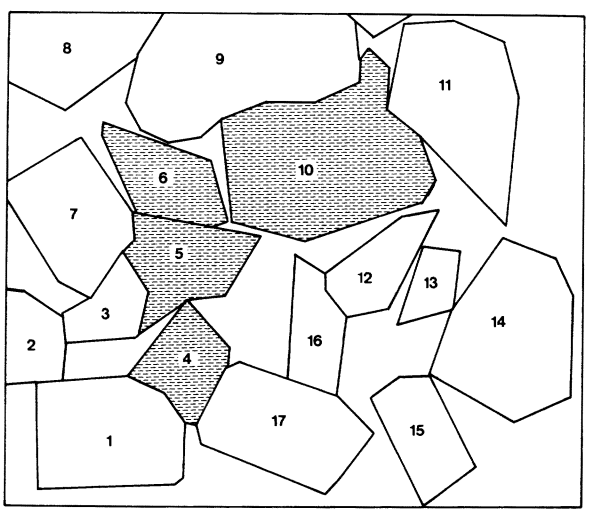

Fig. 3. Song-territories of Willow Warbler males before removal in 1978. Territories of removed males (no. 4, 5, 6, 10) shaded.

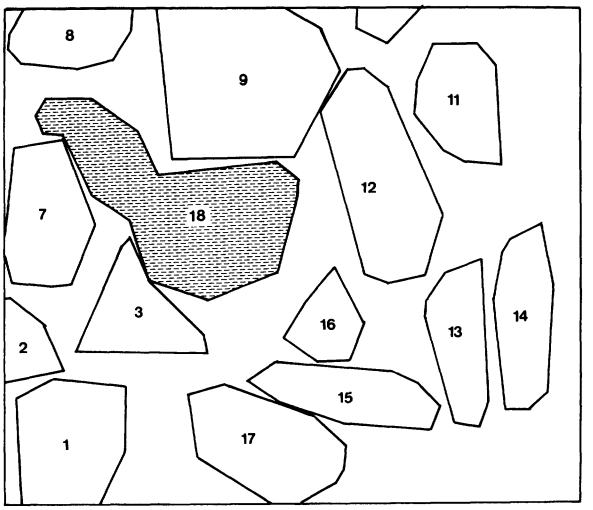

Fig. 4. Song-territories of Willow Warbler males after removal in 1978. Territories numbered as in Fig. 3. The territory of the new male (no. 18) shaded.

3). Some days after the removal a new male occupied part of the emptied area including also some areas not previously occupied by any other male. The neighbouring territory owners enlarged their territories also in this year (Fig. 4). The new male was very aggressive and active in territorial defense. No other females but those incubating at the time of removal were seen in the area. We have no indications that the new male ever mated.

Discussion

The results show that the aggression of the territorial Willow Warbler males excludes other males of the same species from establishing territories, at least from the middle of the incubation period. In control areas no new males established territories. During the two preceding years, when territories were mapped and controlled during the whole breeding cycle no new male appeared despite the fact that more than 30% of the investigation area was vacant in these years (Arvidsson and Klaesson unpubl.). Either there were no non-territorial males in these years, which is less probable, or this 30% of the area was not suitable for the Willow Warblers. It is obvious that at least one of the stationary males must disappear if a new male should have any chance to establish a territory after the onset of breeding. This is consistent with the findings of Davies (1978) and Krebs (1982).

Both years the density of males was lowered because only one new male replaced the 3 and 4 males, respectively, that were removed. The reason for this may be the neighbouring territory owners' interest to enlarge their territories or that the pressure from "floaters" was low in these years or at the time of the removal. In many other removal experiments the number of territories did not change significantly (Watson 1965, Watson and Jenkins 1968, Holmes 1970, Young 1970, Krebs 1971, Thompson 1977, Wesolowski 1981). In a removal experiment on Song Sparrows *Melospiza melodia* at Reifel Island, Canada, Knapton and Krebs (1974) found that the density of males was not changed if the birds were removed one at a time but if all males were removed at the same time the density was significantly increased. The authors mean that settlement patterns may influence territory size. That the density was lowered in our investigation may partly be due to the late time in the breeding season at which the removals were performed but as females normally are fit to lay eggs until at least the middle of July (Nilsson 1983) this explanation seems less likely. More probable is that the number of non-territorial males in the area was low.

We have no indication where the new males came from. They may have been true "floaters" (Brown 1969) but they may also have been males that, by any reason, lost their mates and failed to get a new female in a former, suboptimal, territory. In a removal experiment on the Great Tit *Parus major* Krebs (1971) found that the new-coming birds emanated from suboptimal hedge-rows surrounding the Wytham Wood. In many other removal experiments the new-comers originated from a stock of young surplus birds (Watson and Jenkins 1968, Harris 1970, Knapton and Krebs 1974).

We got no indication that the male new-comers succeeded to obtain a mate. If no non-breeding females are left in the population the reproductive output is not considerably lowered by the exclusion of some males from breeding. This may actually be the case as it has now been established that polygyny is not uncommon in the Willow Warbler population of Ammarnäs (Bengt Arvidson unpubl.). This seems to be true also for other Willow Warbler populations (Lawn 1978, 1982, Lapschin in Schönfeld 1982, Tiainen 1983). If this is a general phenomenon there is no reason to assume that any female would normally be prevented from breeding. In a removal experiment in Maine, USA, most of the males of the 10 most abundant species removed were replaced but none of the females (Hensley and Cope 1951). In many other removal experiments the result has been the same (for references see Brown 1969). All these results indicate a very low amount, if any, of "floaters" among females. The reason for this may be a widely spread polygyny in many passerine bird species.

Acknowledgements – We are deeply thankful to M. Forsberg and L. Jansson for ringing the males and to Prof. A. Enemar for valuable comments on the manuscript. The fieldwork was supported by grants from Wilhelm and Martina Lundgren Foundation, Elis Vidé Foundation and the Swedish Natural Science Research Council (to A. Enemar).

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Correction!

In Ornis Scand. 14: 3, 1983, page 200 (Carlson, A. and Moreno, J. Sexual size dimorphism and its effect on load size and loading efficiency in Wheatears *Oenanthe oenanthe*), Figure 2 was incorrect.

The correct Figure and legend are given below..

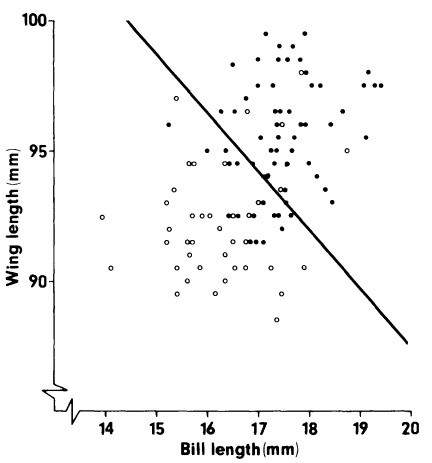

Fig. 2. The wing and bill measurements of the 61 male (black dots) and 40 female (open dots) Wheatears of our sample. The solid line is the calculated discriminant function 39.995 = 0.679 Bill length + 0.302 Wing length.