

# Territory size in a Willow Warbler *Phylloscopus trochilus* population in mountain birch forest in Swedish Lapland

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Territory size of male Willow Warblers in a mountain birch forest varied significantly between years. No correlation was found between the abundance of insects in birches and territory size, but there was a significant negative correlation between territory size and the reproductive output in the previous year. It is unlikely that territory size was directly regulated by food abundance. More likely, competition between males for some resource other than food was the factor regulating territory size. Since weather conditions and predation play a decisive role in the reproductive success of Willow Warblers it is probable that defence of food resources is of little adaptive value.

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## 1. Introduction

In recent years studies of animal territoriality have mainly focused on two questions, viz. the adaptive value of territorial behaviour and optimal territory size (see Wolf 1978, Davies 1978, 1980, Myers et al. 1981 for reviews). Animals should defend territories when this is economical, i.e. when benefits accruing from the exclusive use of some critical resource outweigh the costs of monopolizing it (Brown 1964, 1969, Brown and Orians 1970, Pyke 1979).

By understanding the mechanisms that regulate territory size we may also achieve a better understanding of the adaptive value of territorial behaviour in general. Several models of territory size regulation have been suggested. As animal density often is inversely correlated with the abundance of food, a direct adjustment to this factor has been suggested (Nice 1941, Stimson 1973, Brown 1975, Simon 1975, Wilson 1975). Even if territory size varies considerably, the food content of each territory often is similar (Stenger 1958, Gill and Wolf 1975, Carpenter and MacMillen 1976, Gass et al. 1976, Kodric-Brown and Brown 1978, Gass 1979), and when food is added territories contract (Miller et al. 1970,

Stimson 1973, Slaney and Northcote 1974, Simon 1975, but see also Krebs 1971 and Franzblau and Collins 1981).

Alternatively, animals may respond to habitat composition rather than assess food abundance directly (Hildén 1965, Seastedt and MacLean 1979). Animals “expect” an average level of food in a certain habitat and claim a territory large enough to satisfy their energetic needs.

Both models only take into account the benefits of exclusive use of some critical resource, usually food. But, as pointed out by Brown (1964), territorial defence also implies costs in both time and energy; as a consequence territory size may be adjusted to the density of competitors or intruders (Lack 1966, Stiles and Wolf 1970, Krebs 1971, Schoener 1971, Dunford 1977, Wolf 1978, Myers et al. 1979, Ewald et al. 1980, Norton et al. 1982). An inverse relation between territory size and food abundance could only result from increased intruder density (Myers et al. 1979); habitats rich in resources attract more competitors which makes territorial defence more costly (Krebs 1971, Myers et al. 1979).

Recently several graphical models that combine the

effects of benefits and costs have been proposed (Schoener 1977, Davies 1978, 1980, Kodric-Brown and Brown 1978, MacLean and Seastedt 1979, Tullock 1979, Ebersole 1980, Hixon 1980, Hixon et al. 1983). These models suggest that animals should try to maximize the difference between benefits and costs. Schoener (1983) has discussed different predictions from these models regarding the consequences of a change in food abundance or density of competitors, or both.

In 1974, as part of the LUVRE project (Enemar 1969, 1982), a study of territorial behaviour and breeding ecology of a Willow Warbler *Phylloscopus trochilus* population in mountain birch forest was started at Ammarnäs, Swedish Lapland. About one third of the bird community in this habitat consists of Willow Warblers (Enemar and Sjöstrand 1972). The Willow Warbler's territorial behaviour in general is well documented (Phillips Price 1936, 1961, Kuusisto 1941, May 1947, 1949, Cramp 1955, Brown 1963, Lawn 1982, Schönfeld 1982, Tiainen 1982, 1983a, b, Sæther 1983a, b, Arvidson 1984), but none of these authors discuss the regulation of territory size. In this paper we will discuss how territory size of male Willow Warblers in the breeding season fluctuate between years, with food abundance, and in relation to the reproductive output of the previous year.

## 2. Study area

The area is situated on the birch-covered southern slope of the mountain Kaissats, about 7 km W of Ammarnäs (63°58'N, 16°13'E). A grid of 50 m squares and with a total area of 400 × 600 m was marked out on the slope with coloured plastic strips. To facilitate position determinations, plenty of strips were put up along the borders of each square. In 1975–1978 we mapped the song territories of male Willow Warblers within the study area, and from 1974 through 1978 we measured the reproductive output of the same population (see Arvidson and Nilsson 1983).

The vegetation of the slope consists of birch forest of meadow type, 3–7 m high, with a luxuriant herb layer. Common plant species are *Aconitum septentrionale*, *Lactuca alpina*, *Viola biflora*, *Melampyrum sylvaticum*, *M. pratense*, *Melandrium rubrum* and *Trientalis europaea*. The study area shows a mosaic of wet and dry parts. In moist areas and along streams there are often thickets of willows *Salix* spp. In drier parts junipers *Juniperus communis* are abundant. In the upper part of the area the forest gradually changes into heath type with a less luxuriant shrub and herb vegetation. In the lower part the area consists of a partly drained mire where birches 3–4 m high form screens along the ditches. In undrained parts *Betula nana* and *Salix* spp. grow abundantly. The difference in altitude from the lower to the upper boundary is about 150 m.

The relative abundance of insects found in the birch foliage has been monitored annually since 1967 (An-

dersson and Jonasson 1980) and a preliminary biomass index calculated (Andersson, unpubl.).

## 3. Methods

All Willow Warbler males were ringed with an aluminium ring and an individual combination of colour rings. Most of them were caught in mist-nets soon after their arrival in the beginning of June.

When mapping the song territories, both spontaneous and play-back induced song (Dhondt 1966) were used. To avoid habituation to the play-back song, five different recordings were used. Some males were difficult to activate by the tape-recorded song (cf. Järvi et al. 1980) and in these cases we mostly had to rely on spontaneous song. When the tape-recorded song was played near a territory border two males often appeared. One may argue that mapping with play-back technique makes territories larger than they are in reality. In our study, however, there was no significant difference in size between territories mapped with these two methods (cf. Patterson and Petrinovich 1978).

Territories were delimited by connecting the outermost points to the largest possible polygon. In cases where territories overlapped, the border line was drawn in the middle. All territories were measured with a planimeter with an accuracy of 0.01 ha. Only territories with half or more of their area within the study plot were used in calculations of population density.

## 4. Results

### 4.1. Territory size

Mean territory size varied between 0.52 and 1.14 ha in different years (Tab. 1). The variances are relatively large (C. V. between 29.3 and 53.2%), but the mean territory sizes were significantly different among the years ( $H = 24.125$ ,  $p < 0.001$ , Kruskal-Wallis one-way analysis of variance). The smallest territory measured 0.18 ha (in 1975 and 1977) and the largest (in 1978) 2.38 ha.

Tab. 1. Mean size ( $\pm$ SD) numbers (n), range, and coefficient of variation (C.V.) of Willow Warbler territories in mountain birch forest in Ammarnäs in 1975–1978.

Year	n	Mean size $\pm$ SD	Range	C.V. (%)
1975 . . . . .	27	0.53 $\pm$ 0.25	0.18–1.28	47.7
1976 . . . . .	23	0.81 $\pm$ 0.29	0.32–1.40	36.1
1977 . . . . .	24	0.52 $\pm$ 0.15	0.18–0.82	29.3
1978 . . . . .	15	1.14 $\pm$ 0.61	0.48–2.38	53.2
1978* . . . . .	25	1.10 $\pm$ 0.56	0.28–2.38	50.9

\* The original area doubled.

#### 4.2. Food abundance

After leafing of the birches in the middle of June male Willow Warblers almost entirely forage in the foliage (Sæther 1982, Lennerstedt 1983, pers. obs.). The stomach contents of nine Willow Warblers taken in the beginning of July indicate that most insect species found in the foliage of birches are used as food (Fig. 1). The fact that thrips (Thysanoptera) are missing in the stomachs is probably because they are too small to be profitably exploited, or because they are digested very quickly, if taken by the birds. The Willow Warbler obviously takes a broad spectrum of the available insect species (Kuusisto 1941). In years with mass occurrence of *Epirrita* caterpillars, these are taken in great numbers (pers. obs.).

There was no correlation between territory size and the abundance of insects in the birches (Fig. 2,  $r_s = -0.2$ ,  $p > 0.05$ , Spearman rank correlation test). Nor was there any significant correlation between insect abundance and the reproductive output (Tab. 2,  $r_s =$

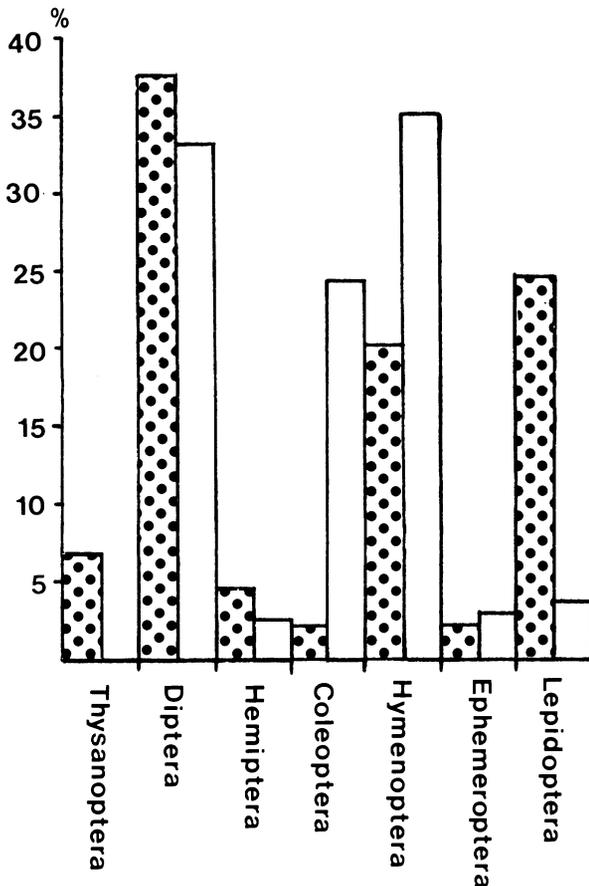


Fig. 1. Approximate proportion (biomass, wet weight) of different insect orders in the stomachs of nine Willow Warblers collected in 1977 (unfilled bars) and on birches (dotted bars; data from Andersson unpubl.) in the same year. Insect orders with less than 1% of the total biomass not included.

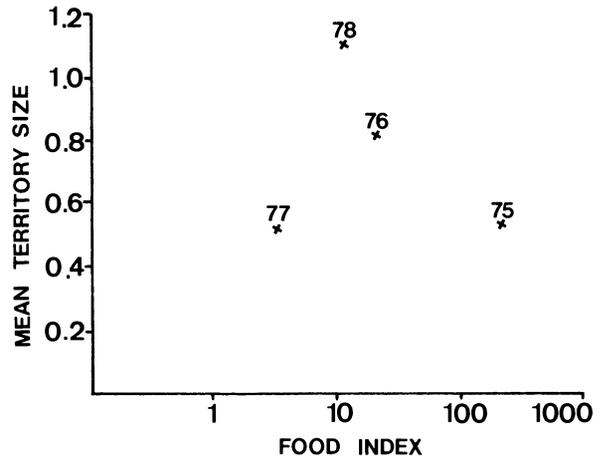


Fig. 2. Mean territory size (ha) of Willow Warbler males as a function of insect abundance on birches.

0.64,  $p > 0.05$ ). Factors such as predation pressure (weasel *Mustela nivalis* was abundant in 1975) and weather conditions (the 1977 summer was cold and rainy) have a strong impact on the reproductive output of the Willow Warbler. Even in years with a low abundance of insects (e.g. 1976) the Willow Warblers produce large broods.

#### 4.3. Population density and territory size

Since the territory size of Willow Warbler males seems to be little influenced by food abundance, the size may merely reflect the number of conspecific males trying to establish territories in the same area. It is difficult to measure the number of returning males in spring, but mean territory size was significantly negatively correlated with the reproductive output of the previous year (Fig. 3,  $r_s = -1.0$ ,  $p = 0.05$ ). Provided that male mortality during migration and in the winter quarters is rather constant between years and that the reproductive output measured in our study area is representative of the population from which the males were recruited, this could be interpreted as territory size being regulated by the costs of territorial defence; after years with a high reproductive output territories get smaller due to higher defence costs, and after years with a low reproductive output territories get larger due to lower defence costs. Breeding density and mean territory size

Tab. 2. Index of the amount of food available in birches (from Andersson unpubl.) and reproductive output (no. of fledglings female<sup>-1</sup>) of Willow Warblers in mountain birch forest at Amarnäs in 1974–1978.

	1974	1975	1976	1977	1978
Food index . . . . .	331	260	38	5	13
Reproductive output . .	3.3	2.4	4.4	1.6	2.3

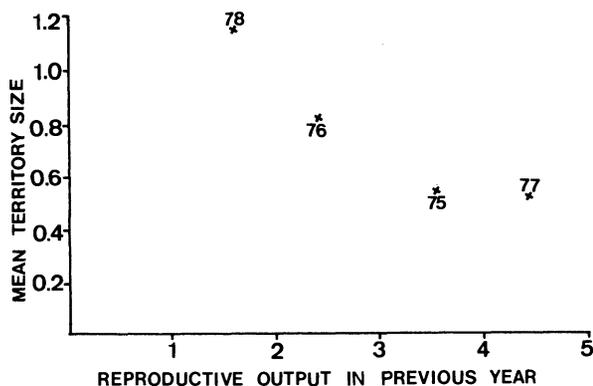


Fig. 3. Mean territory size (ha) of Willow Warbler males as a function of reproductive output (no. of fledglings female<sup>-1</sup>) in the previous year.

were not significantly correlated, however (Fig. 4,  $r_s = 0.8$ ,  $p > 0.05$ ), but this is probably because sample size is too small (i.e. only four years). To some extent it may also have been an effect of a slightly different habitat utilization in different years (Tab. 3).

## 5. Discussion

### 5.1. Insect abundance and territory size

A direct adjustment of territory size to food abundance has frequently been suggested (Nice 1941, Stenger 1958, Cody and Cody 1972, Stimson 1973, Slaney and Northcote 1974, Brown 1975, Simon 1975, Wilson 1975). Such a model predicts an inverse relationship between territory size and the amount of available food.

In the mountain birch forest at Ammarnäs the abundance of insects varies considerably between years, mainly because of massive outbreaks of *Epirrita* caterpillars in some years (Andersson and Jonasson 1980). Our analysis of the contents of nine Willow Warbler stomachs, together with direct observations, indicate that the Willow Warbler males are able to exploit most

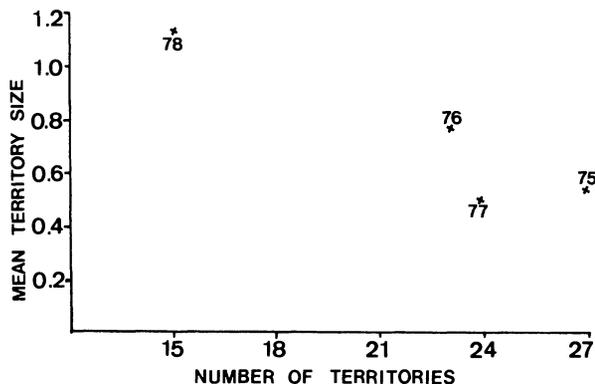


Fig. 4. Mean territory size (ha) of Willow Warbler males as a function of male density within the study area.

Tab. 3. Habitat utilization of Willow Warbler males in mountain birch forest at Ammarnäs in 1975–1978.

	1975	1976	1977	1978	1978
Censused area (ha) . . .	22	24	21	24	43
Unsuitable area (ha) . . . . .	2	2	2	2	3
Utilized area (ha) . . . . .	13.1	14.7	11.0	14.4	27.6
% of suitable area utilized . . . . .	66	67	58	66	69
No. of territories . . . . .	27	23	24	15	25

types of insects found in the foliage of birch, which is also strongly supported by studies in Finland (Kuusisto 1941). Since the amount of insects varied considerably from year to year, we would expect territory size to vary in the opposite direction if a direct adjustment to food abundance took place. However, we could find no support for this hypothesis; there was no correlation between the abundance of insects in the birches and territory size. Apparently, the Willow Warbler males did not respond to changes in food abundance by adjusting their territory size.

Some other studies point in the same direction. Krebs (1971) could not find any inverse relation between food and territory size in an experimental study of Great Tits *Parus major* and considered interactions between males to be responsible for differences in territory size. Franzblau and Collins (1980) tried to influence territory size in a breeding population of Rufous-sided Towhee *Pipilo erythrophthalmus montanus* by increasing the amount of available food experimentally, but were unable to manipulate the defended area in this way.

The fact that no inverse relation was found between insect abundance and the size of the defended area in our Willow Warbler males, contrary to the situation in many species studied in the non-breeding season (Gill and Wolf 1975, Carpenter and MacMillen 1976, Gass et al. 1976, Kodric-Brown and Brown 1978, Gass 1979, Myers et al. 1979, Davies and Houston 1981), is not surprising, since the main goal of males in the breeding season is to monopolize resources in order to obtain a mate (or mates) and to produce offspring (Emlen and Oring 1977). Males should try to monopolize areas with an overall high quality, and food is but one possible factor that is important for attracting a mate and rearing offspring. Other quality factors could be safe nesting sites and cover for both adults and newly fledged offspring (Tinbergen et al. 1967, Horn 1968). In the birch forest at Ammarnäs the Merlin *Falco columbarius* preys heavily on newly fledged Willow Warblers (Hård and Ene-mar 1980), which indicates that protection against predators may be important.

The lack of an inverse correlation between insect abundance and territory size does not, however, exclude food as a possible determinant of territory size in

Willow Warbler males. It seems reasonable to assume that the amount of available energy on their arrival in spring could influence the males' time budgets and thereby also affect the time available for other activities such as territorial encounters. In years when food is scarce the males must spend more time foraging and can devote less time to other activities such as territory defence. In years when food is abundant the males may use more time in territorial disputes. Unfortunately we have no figures on the amount of insects available at the time the males arrive and it is therefore at present impossible to test this idea.

The alternative, i.e. that males should respond to habitat composition rather than assessing food abundance directly (Seastedt and MacLean 1979), predicts a mean territory size that varies little between years. In our study the mean territory size varied significantly between years, which indicates that this model can be excluded.

## 5.2. Density of males and territory size

As territorial defence implies costs both in time and energy, territory size may be regulated by the number of conspecific intruders (Lack 1966, Krebs 1971, Dunford 1977, Myers et al. 1979, Ewald et al. 1980, Norton et al. 1982). Areas rich in critical resources attract more competitors and thus make territorial defence more expensive (Krebs 1971, Myers et al. 1979).

In a study of wintering Sanderlings *Calidris alba*, Myers et al. (1979) found that, once the interaction of prey density and intruder pressure had been controlled for statistically, food density had no effect on territory size. Likewise, when food was provided at a constant level, changes in the territory size of Black-chinned Hummingbirds *Archilocus alexandri* resulted from changes in intrusion pressure (Norton et al. 1982), and the same seems to apply in many wintering nectarivores (Kodric-Brown and Brown 1978, Gass 1979) and in Pied Wagtails *Motacilla alba* (Davies and Houston 1981).

Also in breeding birds territory size may be controlled by intrusion pressure. Ewald et al. (1980) found an inverse correlation between intrusion pressure and territory size in a colony of Western Gull *Larus occidentalis*. In this case, variations in food abundance could not have caused the variations in territory size since the gulls did not feed within their territories.

Assuming that the number of Willow Warbler males returning in spring is proportional to the number of offspring produced in the previous breeding season, we may predict an inverse relation between territory size and reproduction output in the previous year; this was exactly what we found. This indicates that the costs of territorial defence may be a strong determinant of optimal territory size in Willow Warbler males in the breeding season. The higher density of competing males may also depress the amount of energy available to each male (cf. Charnov et al. 1976). This could force males to

spend more time foraging in order to obtain sufficient amounts of energy and allow them less time for territorial encounters. The combined effects of higher defence costs and less available energy should be a smaller territory that would be less expensive to defend both with regard to time and energy.

Some other studies of breeding birds also suggest an inverse relation between the number of offspring produced in one season and territory size in the next. Miller et al. (1970) demonstrated that the number of territories increased in years following successful reproduction in Red Grouse *Lagopus l. scoticus*. According to Watson and Moss (1970) the same applies to the Great Tit *Parus major* population studied by Lack (1966).

Our results, although incomplete, indicate that song territory size in Willow Warbler males is determined by the density of competing males rather than by the density of food. We can however not exclude the possibility that the amount of energy available on the males' arrival at the breeding grounds may influence territory size. Furthermore, the density of Willow Warblers probably influences the amount of food available to each male, resulting in a change in the males' time budgets. Future studies of time and energy budgets of Willow Warbler males are necessary to better understand the regulation of territory size in this species.

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