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Accuracy and efficiency of mapping territorial willow warblers Phylloscopus trochilus: a case study

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The number and distribution of willow warbler territories were established in a study plot of 15 ha in a subalpine birch forest by trapping and colour-ringing the male birds. The size and form of the territories were estimated by identifying and plotting the ringed males and their movements. The bird community was independently censused by application of the mapping method according to international recommendations. Fifteen males were ringed and found to be territorial and fifteen males were stationary according to the mapping census. The distribution of the stationary males (the mapped clusters) conformed largely with that of the territories, although the correspondence was not complete. The mapping census showed a slight tendency to produce two clusters within territories. The "mapping efficiency" was 71 ± 20% (mean number of observations in the clusters, as a percentage ± S.D., of the maximum possible).

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Число и распределение участков пеноски-веснички было установлено на территории в 15 га путем отлова и кольцевания самцов. Размеры и форма участков определялись на основе идентификации птиц и картирования находок окольцованных самцов и их передвижений на участке. Независимо проводили перепись состава птиц применением картографического метода по международным рекомендациям. 15 самцов были окольцованы, установлена их территориальная приуроченность, и 15 самцов оказались стационарными по картированной переписи. Распределение стационарных самцов (картированная группа) в основных чертах совпадает с распределением территориальных птиц, но не соответствует ему полностью. Перепись обнаружила слабую тенденцию к формированию 2-х групп внутри территории. Эффективность картирования составляет 71 ± 20% (среднее число наблюдений в группах ± стандартное отклонение, отнесенное к максимально возможному количеству птиц).

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1. Introduction

In a previous two-year study the number of mapped territories of passerines was compared with the number of nests found in a census plot of 15 ha in a subalpine birch forest (Enemar et al. 1976). Only two species were sufficiently abundant to give fairly reliable information on the species-specific accuracy of the mapping method, namely the brambling *Fringilla montifringilla* which was underestimated by territory mapping, and the willow warbler *Phylloscopus trochilus* which was overestimated. The number of nests, however, is of limited value in such comparisons for two main reasons (often forgotten by students of the methodology of the mapping method): (1) The mapping method applies to the stationary (permanently territorial) birds, whether breeding or not, and therefore the significance of an indicated overestimation is not possible to interpret, even when all nests have in fact been located. (2) The distribution of the nests does not fully conform with that of the "song-post areas" of the breeding males, and therefore it is not always possible to decide which nest, if any, belongs to a certain mapped territory (cluster of registrations).

To investigate the accuracy of the mapping method (i.e. the proportion of territories in fact present which were located by mapping) as far as the willow warbler was concerned, territorial mapping was carried out in an area where the number of stationary males was established by colour-ringing and where the extent and distribution of their territories (activity areas) were estimated as carefully as possible. The main aim was to clarify why the previous tests had resulted in overestimation of the population number and also to obtain a reliable estimate of the efficiency of the census work (number of contacts as a percentage of number of census visits). The results are presented in this paper.

2. Methods

The investigation was carried out in the subalpine birch forests on the south-facing slopes of the mountain complex of Gaissatj (Kaissats) and Valle in the Ammarnäs area, Swedish Lapland (65°58′N, 16°13′E) in 1976. The density of birds in this area fluctuates between 250 and 450 territories per km^2, and about 40% of the breeding community consists of willow warblers. This species and its territorial system is currently the object of a special study in an area of 30 ha which was provided throughout with a system of grid marks consisting of coloured plastic bands. The grid size was 50 × 50 m. As a result the observer could at any time determine with sufficient accuracy his own position and the position of the birds registered anywhere in the area.

Two of the authors (P. K. and B. S.) in cooperation with Bengt Arvidsson, Björn Arvidsson, Göran Cederholm, Frank Götmark, and Ingemar Hård af Segerstad concentrated on estimating the number and position of stationary willow warbler males in the area, i.e. the number of territories. This was accomplished by

(1) trapping and colour-ringing all males. An extensive netting programme was performed beginning on 2 June. The males could often be enticed to approach the nets by playing back willow warbler songs on a tape recorder placed under the net;
(2) identifying and plotting the position of the ringed males and their movements on maps of the area. This work went on until 22 June;
(3) plotting the boundaries of the area within which each separate male reacts to and approaches the tape recorder playing back the willow warbler song; and
(4) searching nests and finding out as far as possible to which males the nests belonged.

Most territorial males were colour-ringed before 11 June, the last one on 18 June. The number and distribution of the territorial males could be established on the maps where the information under (2) and (3) above had been entered. The "activity areas" of neighbouring males seldom overlapped, but in those cases where they did, the boundaries were drawn through the centre of the zone of overlap. The "activity areas" of the males demonstrated in that way are here considered to correspond to the male territories.

One of the authors (A. E.) did the census work by applying the mapping method according to the recommendations given by the International Bird Census Committee (Anon. 1969). The size of the plot was 20 ha, consisting of a square of 400 × 500 m located within the area mentioned above. The census-taker was well acquainted with the habitat and its bird community and had good experience of the mapping method, although he had not censused the plot in question before. Ten visits were made to the plot on different mornings during a period of two weeks, the first and last visits on 10 and 23 June, respectively. This means that the census work was carried out during the nest-building, egg-laying and part of the incubation period of the species. The census work started between 0420 and 0800 hours (mean 0650) and lasted for 144 ± 33 min (mean ± S.D.). The whole community of birds was mapped and the total number of stationary males was estimated to be 52 (260 territories per km^2), belonging to 13 species.

All ten visits were considered valid for mapping the population of stationary willow warblers. Three registrations were required as a minimum before a cluster was accepted as indicating the presence of a stationary male. Following the international recommendations, moreover, a group of registrations was accepted as belonging to two separate territories if there was at least one pair of simultaneous observations of two males, or at least two pairs of non-simultaneous observations.

The mapping census was carried out regardless of whether the birds sighted were ringed or not. Moreover,

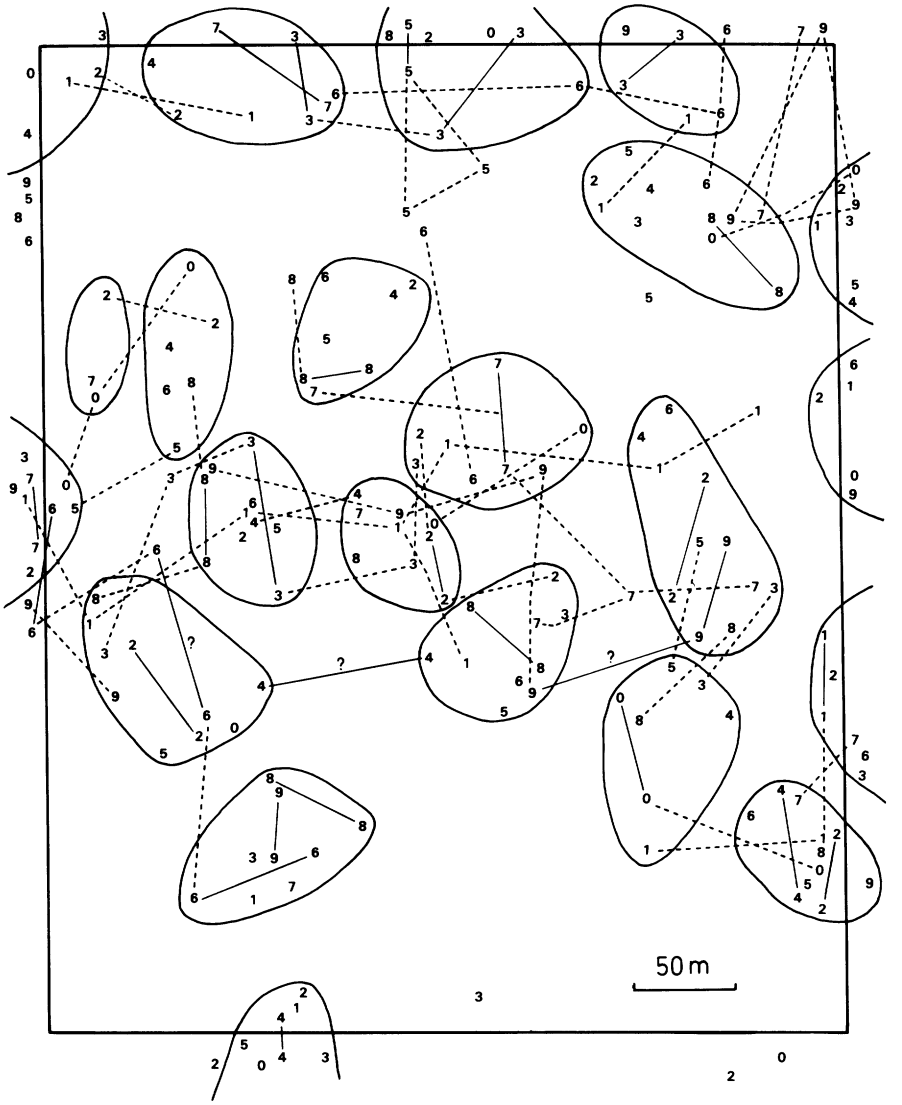

Fig. 1. Distribution of the registrations of willow warblers (figures, indicating the numerical order of the visit when the registration was made. O stands for visit no. 10). Evaluated clusters accepted as indicating the presence of a stationary male are encircled by thin lines. Open circles around edge clusters indicate stationary males which should not be counted to the population of the plot according to the international recommendations. Dotted lines connect simultaneous contacts with two or more males. Full lines indicate observed song-post shifts. A question mark indicates that the observer was uncertain whether a pair of registrations concerned one or two males.

the censustaker had to present to his co-authors the final evaluation of the species map showing the number and position of the mapped stationary males before he had access to their map showing the distribution of the territories.

3. Results and discussion

3.1. The accuracy of the census work

The territories of the colour-ringed males were considered to belong to the study plot if more than half of the territory was located within the plot. As seen in Fig. 2 the study plot contains 15 territories, in other words, 15 colourringed males were resident there. They are indicated by the capitals A to O on the map. Fig. 1 shows that the number of clusters obtained during the mapping census and accepted as indicating the presence of stationary males is 15 (letters a to o in Fig. 2).

According to the theory of the mapping method the number and distribution of the clusters of registration should conform with those of established territories. It is clearly seen from Fig. 2 to what extent clusters of registrations and territories coincide. In general, agreement is good, although many clusters are somewhat displaced in relation to the territories. However, territory D covers two clusters, d and e. Cluster d is a small one consisting of only three registrations, but it is nonetheless separated from the two adjacent clusters by one and two simultaneous registrations, respectively, and should therefore be considered valid (Fig. 1). Territory M also contains two clusters, although in this case there were no instances of simultaneous registrations, but four non-simultaneous ones (i.e. pairs of registrations made during the same visit but not simultaneously; hence they cannot certainly be said to refer to two different males). As cluster u should not be counted to the population of the study plot according to the rules, this mistake did

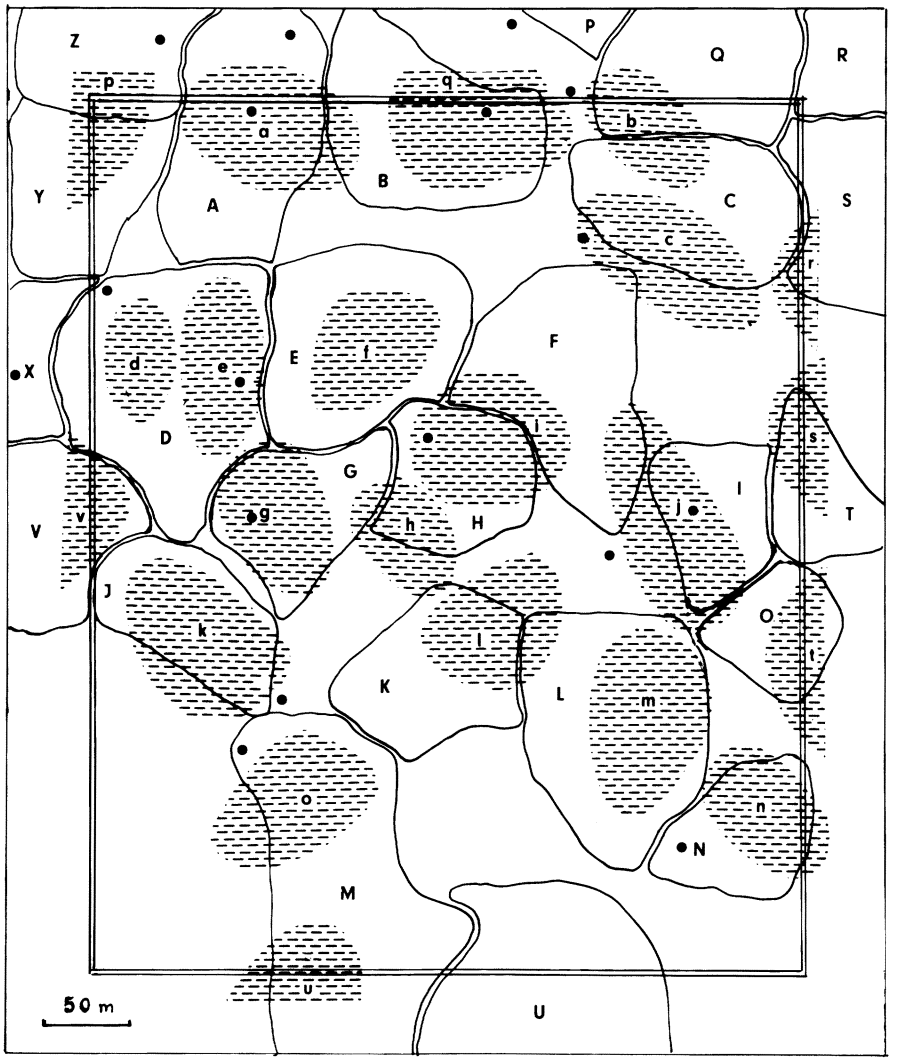

Fig. 2. Map showing the study plot (double-lined boundary), framed by a zone of 50 m outside the plot. The dashed areas correspond to the cluster areas of Fig. 1 (small letters). Thin lines indicate the boundaries of the territories (capitals). The position of the letters in relation to the plot boundary indicates whether or not the territory or the cluster should be referred to the population of the plot. (A thin space is left along the boundaries between adjacent territories only to make the map easier to survey.) Black dots indicate position of found nests.

not affect the mapping result. Nevertheless, what happened in territories D and M may indicate a tendency of the mapping method to overestimate willow warbler territories by recording two clusters of registrations within a territory. Only one territory, the edge territory U, was overlooked by the mapping census.

As expected, cluster and territory of the same male at the edge of the plot could be referred to either side of the plot boundary, thus giving rise to some disagreement between the methods. Clusters q and t are excluded from the plot despite the fact that their corresponding territories, B and O, lay within the plot. This loss is partly compensated by cluster b which should have been excluded from the plot judging from the position of territory Q.

More than half the number of territories and clusters on the plot conform so well in location and distribution that they can reasonably be considered to refer to the same stationary males, namely the pairs A/a, B/q, D/d+e, E/f, G/g, J/k, L/m, N/n, and M/o+u, whereas the overlap is less good for Q/b, C/c, F/i, H/h, I/j, K/l, and O/t. Moreover, even the edge clusters r, s and v show close association with territories. In fact, an alternative pairing including all territories and clusters cannot easily be made. This does not mean that all registrations in a cluster refer to the same colourringed territory owner, not even in cases when the overlap is perfect. Some "intermingling" of the males certainly occurs during census work and subsequent evaluation, which may at least partly explain the displacement of the clusters in relation to the territories. The position and shape of the latter may also be subject to some error. Nevertheless, it is encouraging that such a high degree of agreement occurred.

3.2. The efficiency of the census work

The number of the registrations included in the clusters has been used to calculate the efficiency of the census work, "the mapping efficiency" (Enemar 1959, Williamson 1964, Hogstad 1967, and others). Mysterud (1968) showed by application of the check method that the mapped clusters provide too high an estimate of the efficiency value because the calculation is restricted to those stationary males which give rise to accepted clusters. The stationary population will consequently be underestimated. This bias was avoided in the present investigation because the true number of stationary males was known. When all clusters a to o are used, the calculated efficiency value was 71 ± 20% (mean ± S.D.). The value would be somewhat higher if one cluster of the two in territory D were excluded. The efficiency value is in agreement with that arrived at when willow warblers were mapped in mountain birch forests at Abisko, nothernmost Lapland (74%, Enemar 1963), and in a deciduous wood in southern Sweden (73 ± 14%, Enemar 1959).

Even if the true number of stationary males were known the efficiency value would nonetheless be subject to some error owing to the fact the registered singing males were not individually identified during the census work. It is possible that stationary males have on occasion been included in wrong clusters. This error will affect the standard deviation rather than the mean. Moreover, it is not known to what extent nonstationary visiting males have been included in clusters and how many contacts with stationary males have been designated as surplus registrations (i.e. contacts not included in clusters). Both errors affect the efficiency mean, the last one only to an insignificant extent as the proportion of surplus registrations was small (8% within the plot). Visiting males may increase the efficiency value. They most probably occur in the plot only rarely as all trapped and ringed males appeared to be stationary within the study area, i.e. no males disappeared after ringing. Even if the frequency of such observational errors as double registrations is unknown it seems justified to consider an average efficiency of 70% to be near the true value.

The high efficiency value of the mapping technique for willow warblers is supported by a recent investigation (Järvinen and Lokki 1978). They presented an elucidating analysis of the qualities of the mapping efficiency value by investigating a deterministic model based on assumptions in agreement with the international recommendations for the mapping method. They concluded that the mapping efficiency differs insignificantly from the true efficiency when the latter exceeds 50%. In other words, when the probability of detection is more than 50% practically all stationary males should be expected to be identified by the mapping census. This is in agreement with the results of our experiment.

3.3. The number and distribution of nests

Twelve nests were found within the plot, implying that at least 12 of the 15 males had mated. The male nest-owners could not be identified with certainty in all cases because some females were observed to copulate with more than one male and because the feeding birds could not be examined at all nests. No nests or females were found associated with the males of territories K and O. This is in agreement with the results of previous census experiments when more stationary males were mapped than nests found in a study plot of 15 ha in the same habitat (Enemar et al. 1976). The same investigation also showed that the distribution of the nests did not conform with that of the clusters of registrations. This experience is supported by the present investigation. The map of Fig. 2 shows that the nests are often located outside the territories or clusters. The movements of the breeding females are not restricted to the areas within the territories of their mates during the egg-laying and incubation period, and they obviously also may select nest sites irrespective of the boundaries of these territories (unpubl. obs.). The general conclusion from these results is that interpretational difficulties may well be encountered when the mapping method is tested by comparing the census result with the number and distribution of nests.

In the previous experiments (Enemar et al. 1976) the number of stationary males exceeded that of the nests by a factor of 1.37 and 1.38 in the two seasons of investigation. The same factor appeared to be 1.25 in the present study. Thus the "overestimation" accounted for in the previous experiments may be explained by the presence of non-breeding stationary males. But it is also clear that this might not be the whole explanation. Evidently the mapping procedure shows a tendency to produce a small proportion of false clusters as far as the willow warbler is concerned.

4. Final remarks

The general opinion seems to be that the mapping method underestimates most bird populations (Snow 1965, Haukioja 1968, Bell et al. 1973, Slagsvold 1973, Jensen 1974, Mannes and Alpers 1975, Nilsson 1977, Witkowski and Ranoszek 1978). Moreover, in the subalpine birch forests considerably fewer brambling territories were mapped than nests found, and the tendency was the same for more sparsely occurring species (Enemar et al. 1976). Overestimates have also been recorded in a few other investigations (Williamson 1971). Møller (1975), based on a careful four-year study, compared the number of nests found with the results of mapping censuses in a small plot of 9.5 ha in a mixed wood, and found that the census results exceeded the number of nests found by 18% (average of all

species). When considering these contradictory experiences from different regions and habitats one should remember that the true number of breeding pairs and stationary males have been established with varying accuracy. The distribution of the census visits over long periods, two months or more in some investigations, certainly introduces additional difficulties owing to the well-known fact that the changes in the number and distribution of stationary males and nests increases with the length of the census period (cf. Tomialojć 1974, Cyr 1978).

Many authors have claimed that careful studies of the reliability of the mapping method are badly needed to evaluate, among other things, its applicability when absolute population estimates are aimed at. As indicated by numerous studies, low census efficiency in combination with registrational errors during the census work, as well as interpretational errors (Svensson 1974, Best 1975), biases the results in different directions and to a varying extent depending on species, habitat, observer skill, and so on. Convincing methodological investigations, however, are rarely found in the literature (Berthold 1976). One of the main obstacles to overcome is to obtain correct information about the number and distribution of territories of species populations which are large enough to permit conclusive comparisons with census results to be made. (It is amazing to see how some authors attach importance to whether a species consisting of only one pair in a study plot has been overlooked or represented by one or two territories in the census results; sometimes percental shares have been calculated on such information). The present experiment is based on a species population of a size that probably fulfils these requirements.

Although the census procedure shows a tendency to overestimate the numbers, it seems justifiable to conclude that censusing willow warblers in the subalpine birch forests by application of the mapping method provides results which are near the true numbers of permanently territorial males, all the more as the results are very similar to those obtained from earlier preliminary investigations in the same habitat. This conclusion should not, however, be considered generally valid for the species in all habitats.

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