

What is the true breeding bird population of a census area?

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The bird population of an area in SE Finland was censused by almost daily mapping from 13 May to 31 July 1981. The size of the area is 16 ha: 12 ha forest, 2 ha dense young tree plantations and 2 ha meadows. Mixed coniferous forest of medium productivity is the dominant habitat type. During the main breeding season, June, the number of inhabited territories, summed up for 5-day periods, varied between 48 and 57. The total was 66. During earlier summers at least 30 pairs nested in places not covered by territories of pairs or single males resident in 1981. Thus the carrying capacity of the area is about 100 breeding pairs, twice the number present in any period of the main breeding season. The significance of predation in the numbers of birds is briefly discussed.

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Introduction

In 1930 I published a study on the breeding bird fauna of the main forest types of southern Finland, based on a great number of homogeneous census plots of known size. A review of current concepts of plant and animal communities and of the scanty earlier census studies was included (Palmgren 1930, preliminary report 1928). My field work in the years 1926—28 was carried out by walking across the areas studied along parallel lines at about 50 m intervals. A census repeated 4 times seemed to yield a result very near the true number of pairs. A reliable estimate of the true population density was supposed to be reached if the results of one, two or three census walks were increased by a factor of 1.6, 1.5 and 1.3, respectively. In 1930 I repeated the study of two earlier census plots (Palmgren 1933), this time mapping the birds in their territories day by day, a method proposed by Nicholson (1931) and later used by many ornithologists

(cf. methodological remarks by Hogstad 1967, Mysterud 1968, Enemar et al. 1973, Slagsvold 1973, Nilsson 1977). In the main the results confirmed my earlier estimates of the population density of the two areas.

Since then, interest in census work has increased and the number of papers published is already remarkable, as shown by Berthold's (1976) and Ralph & Scott's (1981) exhaustive reviews (cf. also Enemar 1959). In Finland the line transect method has been the method of choice since Merikallio's work (1946). Mention may be made of the papers by Järvinen et al. (1975—78). The reliability of the results has, however, been questioned (Hildén 1979, 1981, Lehtonen 1979).

Even if a census method yielding absolutely correct results at a given moment could be found, every experienced bird watcher is aware of the fact that the bird community in a given area is in a state of flux, but this problem has not aroused very much

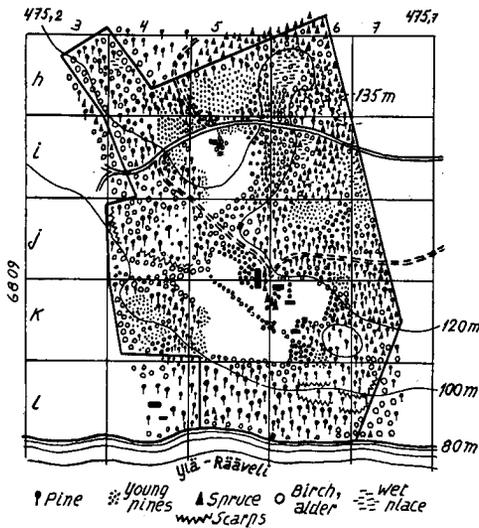


FIG. 1. Habitats of the study area.

interest. The purpose of the present study is to throw some light on the role of such changes in the course of the season.

Study area and methods

The field work was carried out in 1981 on my estate Mäkelä (village district of Hietaniemi in Mäntyharju commune, 61°24'N, 26°32'E; Fig. 1). The place is a small farm, abandoned in the late 1950s and bought by me in 1963. Of the area, 16 ha, 4 ha were originally cultivated, but 2 ha have now been afforested and bear dense plantations of pine, spruce or birch. The forest consists partly of mature pine (squares 15—16, patches of i4 and j4), partly of mixed pine-spruce forest of rather uneven age composition, density and height. Small areas are covered by stands of pure spruce, birch or alder (*Alnus incana*). The productivity level may be indicated by the forest type classification of Finnish forestry: low productivity (*Calluna* type) at the border between squares h4 and i4 and between k6 and l6, medium productivity (*Vaccinium* type) in the shore forest, good productivity (*Myrtillus* type viz. *Oxalis-Myrtillus* type) in most of the forest area, high productivity (*Oxalis-Majanthemum* type and Fern type) in small areas: southernmost part of j4, central part of h6. The highest hills

are rocky with scattered pines. The newly afforested areas are of course not yet well suited for nest building. Despite the small size of the estate, the altitudinal differences reach 55 m. As seen in Fig. 1, the vegetation affords marked edge effects, favourable to the birds. The 20—25 m high "home spruces" form a prominent feature of the landscape. They attract territorially singing males, including those whose territories have their main extension far away from these trees: a Siskin *Carduelis spinus* (nest probably somewhere in k17), Redwings *Turdus iliacus* j4—5 and k5—6, a Dunnock *Prunella modularis*. Later in the summer they were the favourite haunts of Crested Tits *Parus cristatus* and Goldcrests *Regulus regulus*.

The census work started on 13 May and was pursued almost daily until the end of July. Unfortunately the weather this summer was rather bad, especially during the principal breeding time, with low temperatures, frequent rain and almost constant hard wind, which, as is well known, seriously hampers the observation of birds in the foliage. The open fields divide the estate into a western and an eastern part. Both were generally censused by walking from south to north and back along routes 50—60 metres apart, one part in the morning, the other in the afternoon, and always with frequent pauses for listening and looking out for birds moving in the trees. The shore forest slope was studied separately. Every bird observed was recorded with reference to the grid system in Fig. 1. If two males of the same species were recorded singing simultaneously, a special note was made of this. The notes were later entered into simplified copies of the map, one for every species and for every 5-day period, and with special signs for singing male, silent male, female, parents giving warning calls, nest, fledged brood. A dividing line was drawn between the signs for individuals observed simultaneously. Movement of an individual from one place to another was also indicated. Examples of such maps are given (Fig. 2). Cases of apparent transfer to a new territory or enlargement of the territory are noted in the map texts.

I want to emphasize some sources of error. A marked deafness for higher tones in my left ear may render rapid location of a bird difficult and necessitate repeated checking, with risk of the object disappearing. It was impossible to include catching and ringing of birds in my programme. Supposed cases of territory change could thus not be proved, nor could non-territorial birds be distinguished. The bad weather apparently caused an unusual heavy loss of broods (also mentioned in newspaper writings). This of course diminished the exactness of delimitation of the territories.

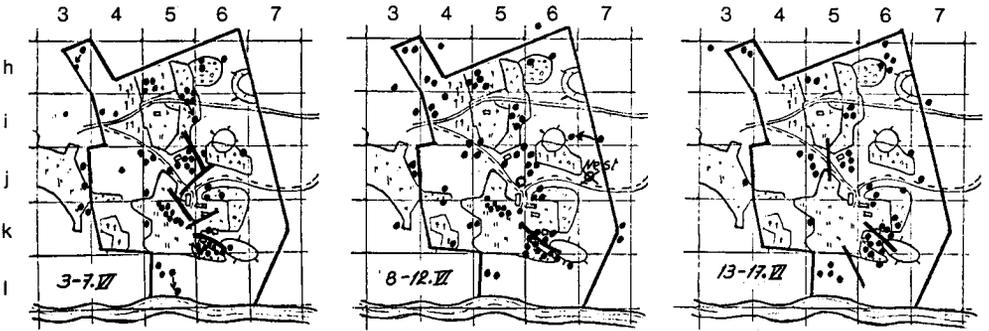


FIG. 2. Observations of the Willow Warbler *Phylloscopus trochilus* during three successive 5-day periods.

Results

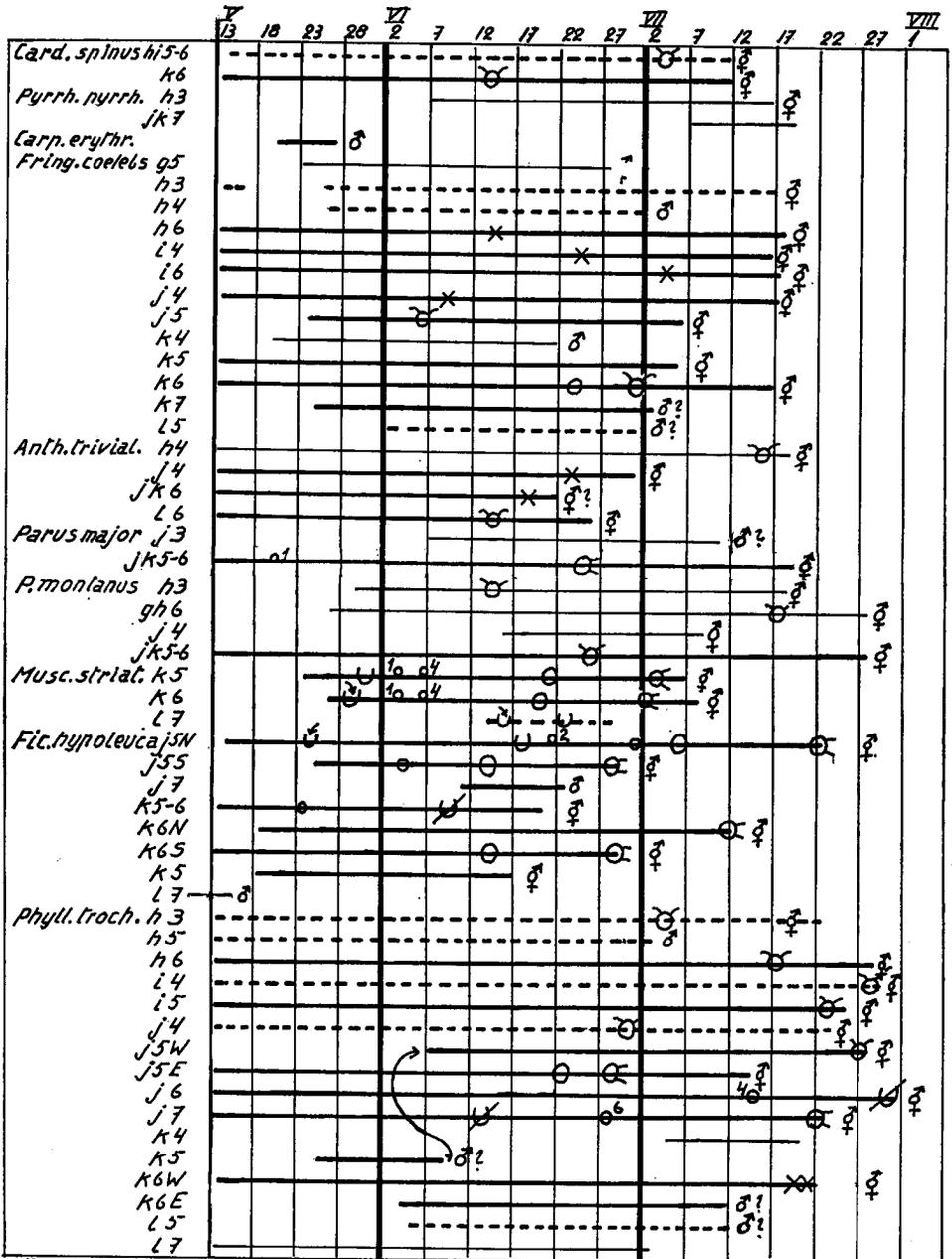
The results of my census work (with the reservations mentioned above) are summed up in Figs. 3 and 4. It is hardly necessary to mention that if no specimen of a bird species was observed during, say, 2—3 days in a supposed territory, this could not be interpreted as true absence, so a continuous line was drawn in the diagrammatic representation in Fig. 3. In a few cases it was impossible to decide with certainty, whether a territory really had an independent existence or was visited more or less regularly by birds from adjoining territories. It is well known that the borders of territories are often very diffuse and that nests can be located at the periphery or even outside the singing range of the male. Such was the case with the Redwing k4—6: the male almost always used the high "home spruces" as singing trees, the nest was at the extreme western border of square k5, but the male was never seen there.

The bird population dealt with in this study can be divided into three categories: (1) pairs or single males holding territories completely included in the study area, (2) birds with terri-

teries at least half of which belongs to the area (if the nest was found within the border the pair was assigned to this group even if the birds spent most of their time outside the study area), and (3) birds only occasionally entering the area. In the totals seen at the bottom of Fig. 3, the last category is not taken into account and the second group is represented by the value 0.5 for a territory. Unmated males are counted as full breeding units.

Discussion

Before the discussion of the general results of the census, a few words may be needed on a perhaps unexpected feature of the diagrams in Fig. 3. The breeding stock of the Chaffinch *Fringilla coelebs* and the Willow Warbler *Phylloscopus trochilus* seem to have been more stable than the populations of some other birds, especially the Pied Flycatcher *Ficedula hypoleuca* and the Redwing. There is some possibility that my observations are misleading here. The individual fates of the two first-mentioned species are undoubtedly more difficult to follow than are the fortunes of the bigger thrushes and the



Explanations:

♂ Unpaired male ⊕ Nest ⊕ Building ✕ Robbed ⊖ Abandoned 1-4 Eggs laid (number?) ⊕ Eggs laid (number?)
 ♀ Pair ⊕ Young ⊕ Young leave nest ⊕ Fledged young ✕ Parents warning ⊕ Pair changing territory

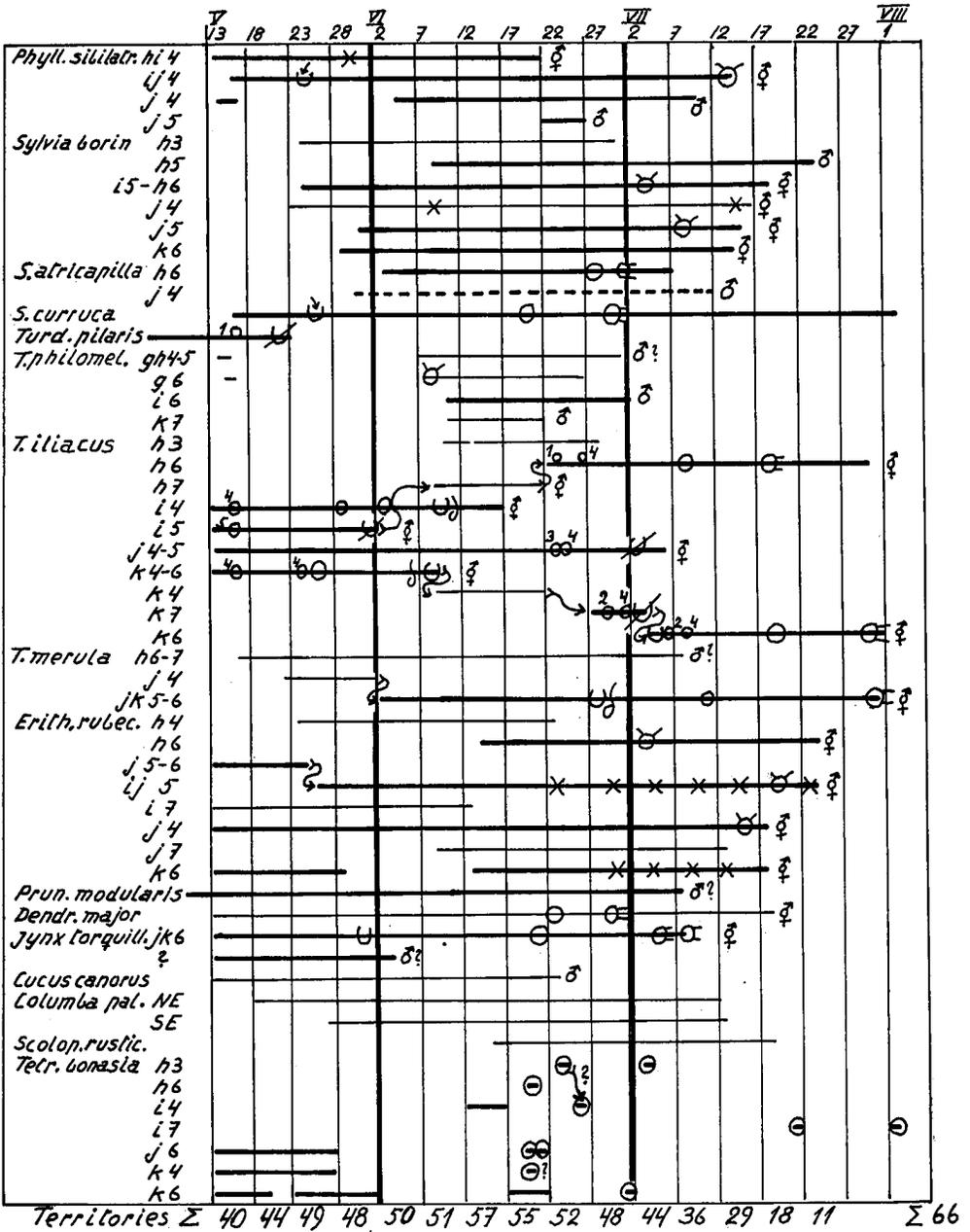


Fig. 3. Synopsis of the breeding population of the study area.

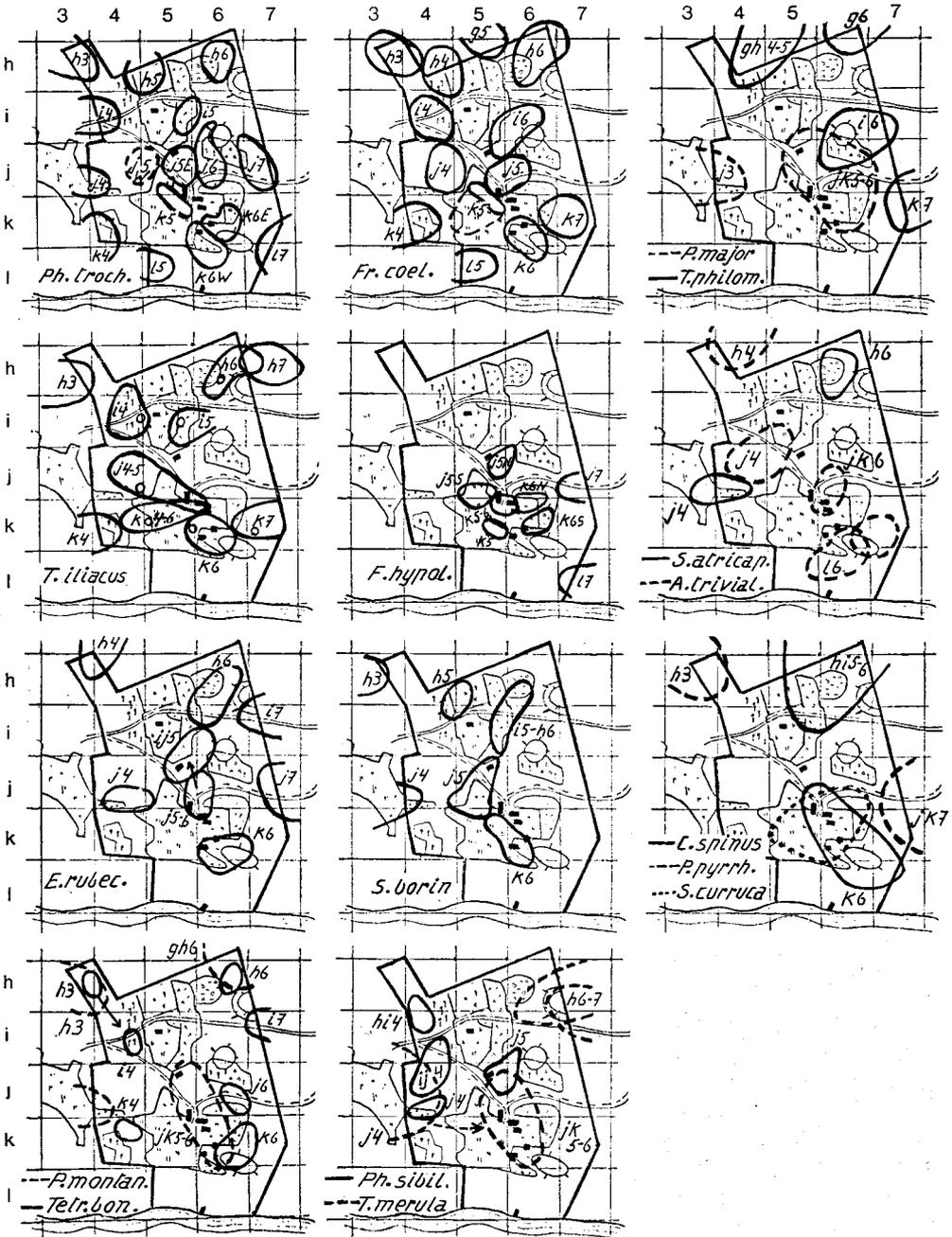


FIG. 4. Territories of the most important species breeding in the study area.

flycatchers breeding in nest-boxes near our house. On the other hand, they are perhaps also more conspicuous to predators. Moreover, being the most common land birds in Finland, the Chaffinch and the Willow Warbler are apparently very well adapted to the environmental conditions and may in fact be more successful than the two other species. Their reserve of unmated individuals is perhaps so big that the loss of a mate in a territory can always be made good immediately.

The sums for the six 5-day periods of June, the peak season for breeding, differ by only 15 % (ranging from 57 to 48) in spite of a fairly lively turnover on the individual plane. But what is the "true breeding population" of the area studied? The sum for all the territories of the first and second categories established during the course of the summer was 66. Is this to be considered the most accurate value? The problem encountered here was formulated in my study of 1933, p. 92 (translation from German): "Is for instance a pair which — like *Turdus musicus* (= *iliacus*) in my spruce forest in 1930 — has built a nest in the spring but disappeared after the nest was robbed to be counted as belonging to the population or not?" In the present study a similar case was presented by a pair of Fieldfares *Turdus pilaris*: the nest was very soon robbed and the birds disappeared somewhere west of the study area, visiting it later only occasionally.

The answer depends on the purpose of the census. If we are primarily interested in the role of the birds as consumers in the system of energy flow, then the actual population density of the habitat at any given time (more exactly the sum of living masses) is the value of interest. From this point of view unpaired males should be counted as single birds, and the census should

also include the young birds with their steady weight increase and general decrease in numbers. I must frankly confess that in spite of recent studies aiming at such a goal (and in spite of my bold presentation of the concept of "Produktionsbiologie" in 1930 and in a preliminary paper in 1928), I believe we still have a very long way to go before we can make a true estimate of the impact of birds on the insect and spider populations. Here, I should like to remind present-day ornithologists of the admirable vision shown by Forbes (1907) as a practical entomologist in starting the linear transect censuses of the bird fauna of Illinois (Forbes 1913, Forbes & Gross 1922).

On the other hand, we may be interested in the capacity of different types of habitats to house birds. In this case the information wanted is the number of territories recorded during the course of the breeding season. The proportion of unmated males is of minor importance. In 1933 I reviewed the data published on unmated males, with the conclusion (p. 94): "The errors caused by proportions of this order of magnitude cannot be considered very important, especially if we argue that a single male with a territory corresponds to a pair in the estimation of the carrying capacity of an area" (translation from German).

From a practical point of view, I would like to stress that the difference between the estimated total population of the season and the populations recorded during each of the 5-day periods in June is fairly small. In every census programme, irrespectively of animal group, we meet the same problem. If the most exact method (or methods) available is applied, the work becomes so time-consuming that the number of samples remains too small to yield the figures of paramount inter-

est: the population densities (and population turnover) of sufficient habitats to represent the region. If we want this kind of information, we have to apply less exact but more rapid methods and find correction coefficients. In the above-mentioned extensive study of 1930, this was my motivation for choosing a census method which, though not very exact, made it possible to cover a great number of study areas. In my opinion a margin of error of $\pm 20\%$ can be considered quite tolerable in ornithological census work.

During the summers of 1964—80 my interest was chiefly devoted to the spider fauna, but I made some bird observations as well. For many species I have records of a fair number of nests located outside the territories occupied in 1981. It is theoretically possible that these sites could not be inhabited by the species under the conditions prevailing in 1981, but this seems extremely improbable and we are certainly justified in counting them as potential territories that chanced to be unoccupied. This assumption adds at least the following numbers of bird pairs to the sum of 66 given in Fig. 3: *Garrulus glandarius* 1, *Pyrrhula pyrrhula* 1, *Anthus trivialis* 1, *Muscicapa striata* 1, *Ficedula hypoleuca* 5, *Regulus regulus* 1, *Phylloscopus collybita* 1, *Ph. sibilatrix* 1, *Turdus pilaris* 3, *T. viscivorus* 1, *T. philomelos* 3, *T. iliacus* 4, *T. merula* 1, *Columba palumbus* 2, *Accipiter nisus* 1, (*Aegolius funereus* 1), *Scolopax rusticola* 2, *Tetrao urogallus* 1, sum = 30, and added to 66 = 96. (The possible number of *Ficedula hypoleuca* is of course chiefly dependent on the number of nest-boxes available.)

The reason why the population did not reach (and in 1964—80 never reached) this carrying capacity is not clear, but this phenomenon is probably general. Migration losses are the most

probable explanation. We also know that there may be severe competition in the wintering regions. It is well known that the wintering European birds can be far more numerous in South Africa than the indigenous birds. Price (1981) has recently demonstrated loss of the wintering territories of a population of the Greenish Warbler *Phylloscopus trochiloides* caused by lumbering in a district in India. Predation during the breeding time plays a role, though probably a minor one. Space does not allow me to discuss this problem further, but the following data on predation may be added.

The nest of a Fieldfare pair on the branch of one of the "home spruces", 25 m from our door, was robbed before my eyes by a Common Buzzard *Buteo buteo* (2 eggs eaten, two left, as the Buzzard was disturbed). The same happened to the nest of the Redwing i5 (with small nestlings) low in a young spruce (also witnessed by me). During my field studies on the Aland islands I was struck by the frequent finds of newly fledged Robins *Erithacus rubecula* in Common Buzzard nests. The large, seemingly clumsy bird moves with astonishing agility flying in dense forest undergrowth. The nest of the Redwing i4 was probably also destroyed by the same Buzzard. The nest of the Redwing i7, with fresh eggs, on a tree trunk in the middle of a small clearing was robbed by an unknown predator.

The Wrynecks *Jynx torquilla* always start their stay in our estate with extensive marauding of nest-boxes. This year one pair and one probably unmated male arrived on about 10 May. The Pied Flycatchers k5—6 and k5 (see, however, below) lost their nests and the breeding of j5N and k6S was much delayed.

A pair of the Great Spotted Woodpecker *Dendrocopos major* has for many years nested in 17 only 10 m from our border. The female hardly ever crosses this border, but the male has been a regular nuisance to the box-breeders. Perhaps it was he (not the Wryneck) who emptied the nest of the Pied Flycatcher k5—6 (eggs eaten). The parents left the territory a week later. This year the woodpecker started its raids relatively late and did less harm than sometimes earlier.

The Jay *Garrulus glandarius* has for some years nested on the estate and comes to feed

there every year. The Spotted Flycatchers *Muscicapa striata* have been especially affected, their losses being easily observed, though none were noted this year.

At least two nests of the Willow Warbler were destroyed by an unknown predator. (Once earlier by an adder *Vipera berus*!)

The following species deserve short comments.

Oriolus oriolus. Heard less than 10 times. Appears every summer but has never nested within our borders.

Parus ater. Sang a few times in the attractive "home spruces", but has never nested in the vicinity.

P. cristatus. The first appeared on 17 June, later frequently seen in the high spruces (as in every summer).

Regulus regulus. In 1981 only occasional observations of apparently non-resident, although sometimes singing individuals. Generally one pair in h6.

Sylvia curruca. During about 10 years a pair (certainly not the same all the time!) has nested in the "home spruces", 6—8 m above the ground. This is another example of the strong attractive effect of the marked feature formed by the towering spruces!

Motacilla alba. A regular visitor (every summer), but has always nested somewhere west of the area. The fields are too small for most other species of open-grounds.

Sturnus vulgaris. The once fairly numerous group of starlings (ca. 10 pairs) gradually disappeared during the years of the sharp decline of the species.

Pernis apivorus. Less often seen than the Common Buzzard. A Honey Buzzard robbed a wasps' nest in a low spruce in a dense plantation.

Tetrao urogallus. A male seen three times, a female also, but this year the brood was encountered east of our border.

Bonasa (Tetrastes) bonasia. Observations of females with chickens were considered to indicate a separate breeding pair only if the age of the chickens excluded confusion with a brood observed earlier.

Selostus: Mikä on laskenta-alueen todellinen pesimälinnusto?

Mäntyharjun kunnassa takseerattiin erään tutkimusalueen pesimälinnusto lähes päivittäisten kartoitusten avulla 13.5.—31.7.1981. Alueen pinta-ala on 16 ha, josta 12 ha metsää, 2 ha tiheää taimistoa ja 2 ha niittyä; eri maastotyyppit ilmenevät kuvasta 1. Korkeuserot alueella ovat peräti 55 m. Esimerkkeinä kartoituk-

sesta ovat pajulinnun laulupaikat kolmena peräkkäisenä jaksena (kuva 2) sekä 17 lajin lopulliset reviiirit (kuva 4).

Pesimäkauden huippuvaiheessa kesäkuussa viiden päivän jaksoissa todettujen reviiirin määrä vaihteli rajoissa 48—57; reviiirin kokonaisuus oli 66 (kuva 3). Aikaisempina vuosina ainakin 30 paria oli pesinyt paikoissa, jotka eivät kuuluneet kesällä 1981 asuttuihin reviiireihin. Näin ollen tutkitun alueen "kantokyky" on n. 100 paria eli kaksi kertaa niin suuri kuin minään jaksena pesimäkauden aikana oli todettu. Vastaus siihen, mikä on alueen todellinen pesimälinnusto, riippuu ratkaisevasti tutkimuksen tavoitteista.

Lopuksi esitetään havaintoja predation merkityksestä tutkimusalueella sekä luettelo siellä aikaisemmin tai tilapäisesti pesineistä lajeista ja vierailijoista.

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