Singing territories and home ranges of breeding Chaffinches: visual observation vs. radio-tracking

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We mapped the singing territories of individually marked Chaffinch males in a 36-ha study plot in southern Finland by visual observation in 1985–87. In addition, we followed the movements of five males with radio-tracking in 1987. The habitat blocks comprising old spruce-dominated forests were almost completely occupied each year, whereas variation in pine-dominated forests was greater. Radio-tracking showed that the males spent a considerable amount of their time outside the singing territories. Home ranges were 4–8 times larger than singing territories and included a broad range of different habitat types. Home ranges also appeared to vary in size and habitat structure from male to male. Territorial males showed no aggressive behaviour towards non-singing males that moved in their singing territory. Our data suggest that "economic" models of bird territoriality are not realistic for the Chaffinch.

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Introduction

We have studied territory selection and the use of space in the Chaffinch *Fringilla coelebs* in an area of boreal coniferous forest in southern Finland in 1985–87. Our aim is to identify environmental factors which are important for small-scale variation both within and between years in the spatial distribution of Chaffinches.

Chaffinch males arrive in southern Finland in the second half of April, about two weeks ahead of the females, and acquire territories where pair-formation then occurs (Mikkonen 1981). Territorial fights are common in the early part of the breeding cycle. As in most forest passerines, territoriality is an important proximate factor that influences local distribution patterns of Chaffinches.

The territorial behaviour of the Chaffinch has been described by several authors (Lack 1941, von Haartman 1947, Bergman 1953, Marler 1956a, b, Udvardy 1956, Glas 1960, Mikkonen 1985), but the descriptions have not been systematic and, therefore, have not been quantifiable either. We have tried to record the territory locations of individual males as well as their movements and habitat use using visual observation and, in 1987, also radio-tracking. Radio-tracking has been applied a few times to studying the movements and behaviour of small passerines (Greig-Smith 1985, East & Hofer 1986), but mainly outside the breeding season.

In particular, we direct attention to such ecologically important aspects of territoriality in the Chaffinch that have not been adequately documented. These include the relationship between habitat variation and how males use their territories and the areas surrounding them. The questions we raise are also relevant for explaining the significance of bird territoriality in general.

Study area and methods

Our study was carried out in the Seitseminen National Park (61°55′N, 23°30′E) in southern Finland. The forest types of the area were described by Haila et al. (1987). The bulk of our data originates from a study plot of 36 ha in the reserve. The plot consists of different forest types, distributed in a mosaic-like fashion: old spruce-dominated forests cover roughly one third, and young coniferous forests about one half of the plot, the rest being covered by small bogs and pine sapling stands (Fig. 1).

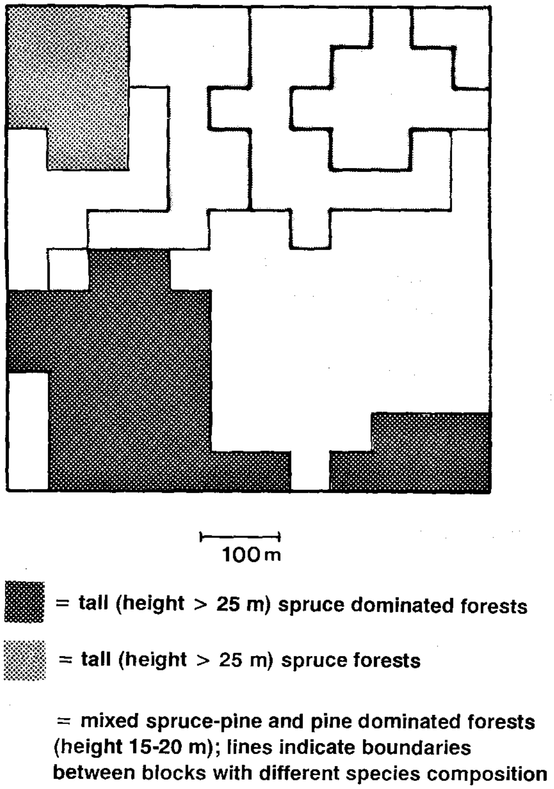


Fig. 1. Blocks of uniform forest types in the study plot. White areas comprise sapling stands or bogs, unsuitable breeding habitats for the Chaffinch.

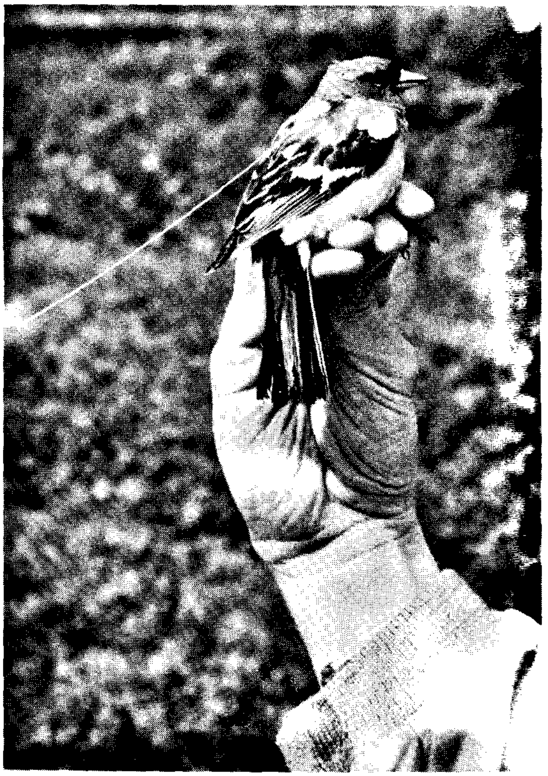


Fig. 2. Radio tag attachment on the back of a Chaffinch male.

The determination of the habitat blocks (Fig. 1) is based on a detailed habitat description of the plot, including the measurements of 28 habitat variables in each 10-m square of the plot. The plot was marked with coordinates in a 25-m grid to facilitate locating observations. We visually observed the movements of males in the plot between 3 May and 25 June in 1985–87, using 10-m squares as units in mapping the observations. We also recorded the activities of the males (singing, calling or foraging) and their vertical position in the vegetation.

In 1987 our method was supplemented with radio-tracking, using similar equipment as described by East & Hofer (1986). Five males (four in our study plot and one in a coniferous forest fragment surrounded by pine, and mixed pine and birch sapling stands, 300 m from the plot) had 1.5-g radio-tags (from Biotrack, UK) attached on their backs with a harness made of cotton-covered elastic (Kenward 1987; Fig. 2). The tracking equipment consisted of a RX-81 receiver (from Televilt, Sweden) with a two-element Yagi antenna. The transmitter signals were audible at a distance of 150–200 m, depending on the topography, the vegetation structure and the bird's height above the ground. The mean duration time of the transmitter batteries was three weeks. Radio-tracking was carried out from 18 May to 15 June and all males were tracked in roughly similar proportions throughout the day.

When starting to track a particular male we walked towards the signal until we got the radio-tagged (and also colour-ringed) male into sight. We then followed the movements and activities of the bird for about half an hour to an hour.

Singing territory vs. home range

Most of our visual observations referred to singing males; consequently, we call territories identified by visual observations as *singing territories*. We defined individual territories by connecting the outermost

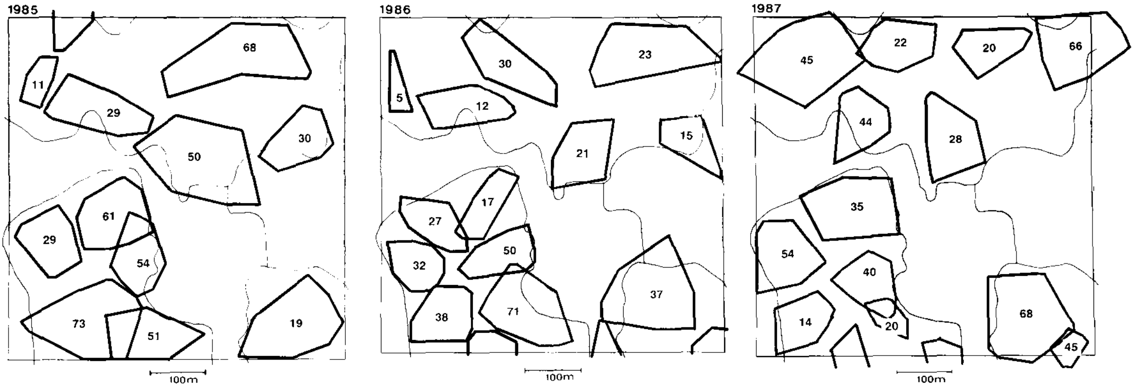


Fig. 3. Singing territories of Chaffinch males in the study plot in 1985–87. The polygons indicate the borders of singing territories (the number of singing observations is given inside each polygon), and the contours border main vegetetion types drawn from aerial photographs.

Table 1. Radio-tagged Chaffinch males (1–5), observation periods, number of observation days and time (in minutes) spent "inside" and "outside" their singing territories (male 1 lost its transmitter after six days). The time budget of male 5 was not calculated because the borders of the singing territory could not be clearly defined (total observation time 279 min).

Male	Observation period	Observation days	"Inside"	"Outside"
1	18–21 May	4	146	7 (5%)
2	18–30 May	9	201	204(50%)
3	21 May–9 June	15	425	247(37%)
4	28 May–15 June	13	646	58 (8%)
5	28 May–10 June	7	–	–

singing observations of each individual male to form a polygon. A total of 11, 13, and 13 males occupied territories in the plot in the breeding seasons of 1985, 1986 and 1987, respectively. Fig. 3 summarizes our data on the location of the singing territories in the three years. The number of singing observations per territory ranged from 5 to 73 (median 32). In calculating these figures, each record at a new singing post was regarded as a separate observation. Except for the four territories with less than 15 observations, the territories were delimited quite reliably. Four, nine and six of the males were colour-ringed in 1985, 1986 and 1987, respectively. The males with colour-rings were distributed over the whole plot, which enhanced individual identification of the other males as well.

The habitat blocks comprising old and tall spruce-dominated forests (Fig. 1) were almost fully occupied each year, whereas variation in the northeastern, mixed pine-dominated parts of the study plot has been greater (Fig. 3).

The singing territories appeared stationary throughout each season. Overlap between different males was slight, the two cases shown on the maps being due to shifts during the breeding cycle.

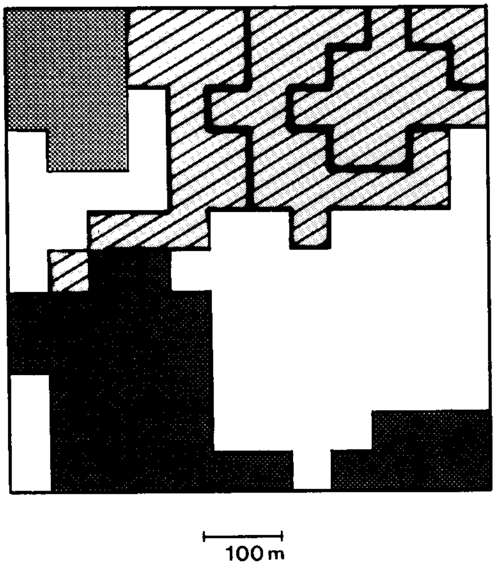
Fig. 4A and Table 1 summarize radio-tracking data on the four males with radio transmitters in the study area in 1987. Male 1 dropped its transmitter only six days after attachment, but the other three males were tracked for about three weeks each.

The males spent considerable amounts of time outside their singing territories. To obtain a conservative estimate, we accepted observations at a distance of more than 50 m from the nearest singing observations as coming from "the outside". The proportion of males being "outside" the singing territory varied from 5 to 50% (Fig. 4A, Table 1). Two of the males (nos. 2 and 3 in Fig. 4A) were beyond the range of the radio signals several times. Male 2 was, by walking to the direction the signals disappeared, found twice at a distance of 300 m from its territory (Fig. 4A) — the location was beyond the range of the radio signals. In other words, the estimates in Table 1 are certainly too low for males 2 and 3.

Fig. 4B shows the movements of the fifth radio-tracked male that held its territory outside the plot. This male roamed in a larger area than the other radio-tagged males, and its singing territory was also larger.

Errata

Due to an editorial mistake Fig. 1 on page 98 and Fig. 4B on page 100 in Ornis Fennica 3/1988 did not reproduce all shades. Please attach these new figures into appropriate places. We apologize the inconvenience this may cause to You.



■ = tall (height > 25 m) spruce dominated forests

▒ = tall (height > 25 m) spruce forests

▨ = mixed spruce-pine and pine dominated forests (height 15-20 m); lines indicate boundaries between blocks with different species composition

Fig. 1

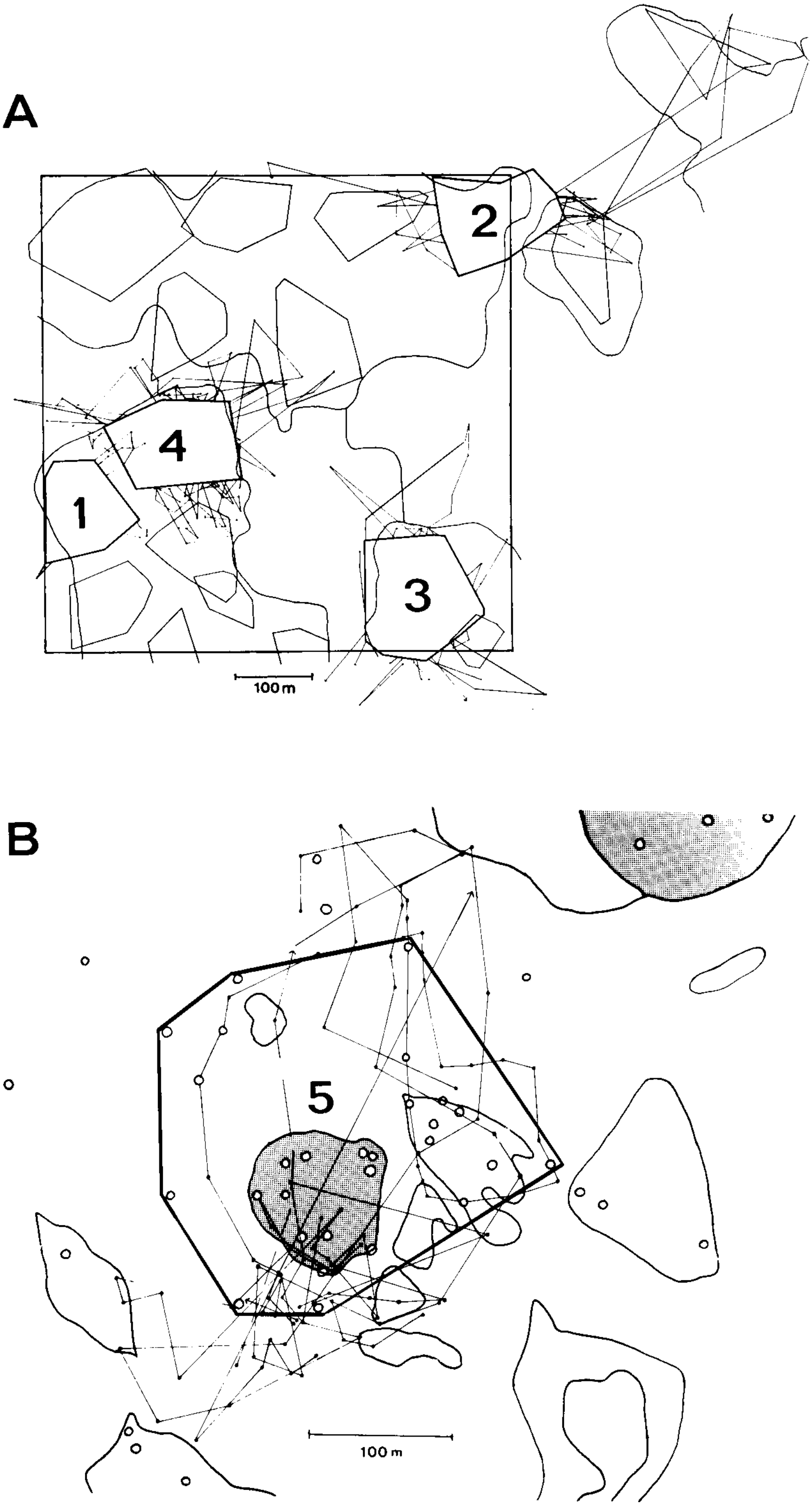


Fig. 4. A. Movements of radio-tagged (shown by thin lines) Chaffinch males 1–4 outside their singing territories in the study plot. Other symbols as in Fig. 3.

B. Movements of radio-tagged (shown by thin lines) Chaffinch male 5. The dark shaded areas indicate high coniferous forests, the lightly shaded young, about 8 m-high mixed forests, and the white area young, low (3–5 m) saplings. The polygon indicates the singing territory and open dots the singing posts of the radio-tagged male and neighbouring males.

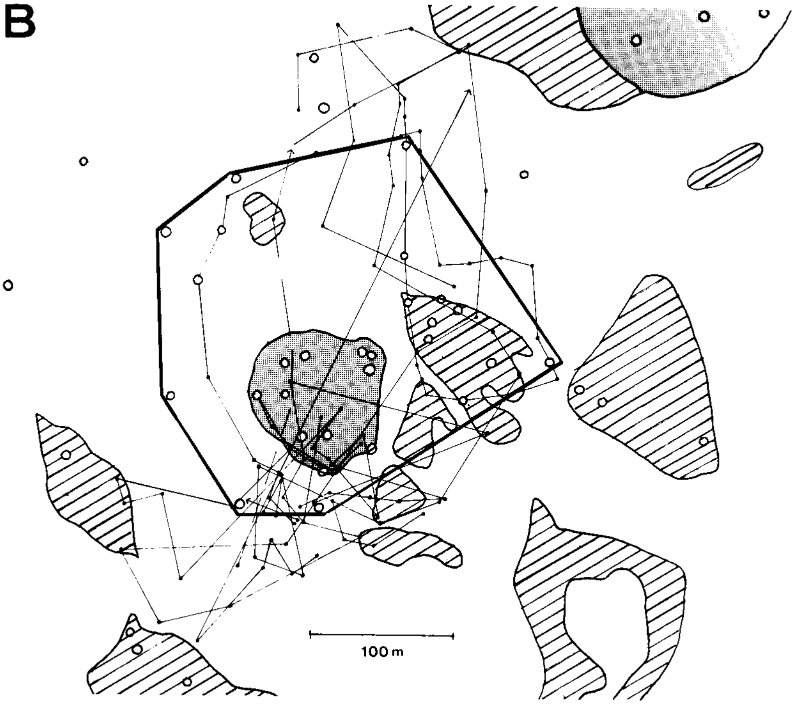


Fig. 4B

When roaming outside their singing territories, the males were silent, only occasionally calling, keeping mainly close to the ground, and they were foraging when seen. Another possible function of moving outside the singing territory might be "stealing" extra copulations (e.g. Birkhead 1987, Møller 1987). However, we acquired no evidence of such a behaviour, and our observations thus agree with those of Schartz & Zimmerman (1971).

Our data suggest a distinction (see also Tryon & MacLean 1980) between the singing territory and the home range in the use of space by Chaffinch males:

(1) The home ranges were 4–8 times larger than the singing territories (Fig. 4).

(2) The home ranges appeared to vary greatly from male to male (Fig. 4).

(3) The home ranges included a great variety of habitat types.

(4) While moving around in their home ranges, the Chaffinch males seemed to be insensitive to the singing territories of the neighbouring males. Each one of the four males tracked in the study plot visited the singing territories of the neighbouring males (and areas beyond them). Nevertheless, no male-male aggressions were recorded in the use of home ranges.

Conclusions

Our experiences emphasize that the following points are important in studying the breeding birds' use of space:

(1) Data collected by visual observations are biased. Only singing posts are adequately represented, but the birds behave differently and move in different areas when they are not singing. In 1985 and 1986 we tried to correct the bias by following individual males as long as possible each time they were detected. However, the birds were initially detected, as a rule, on the basis of singing, and the following records were not independent of the initial singing observation. We nearly always lost a male soon after it ceased singing and moved longer distances at a time. As the singing territory of the Chaffinch seems to be localized and stationary, an essential proportion of the birds' movements is neglected when only singing observations are collected.

(2) This bias is serious also on the level of foraging behaviour, if data are collected on males originally detected by their singing. As an example, we compared in the following tabulation the proportion of Chaffinch male observations on the ground, compared with in the foliage, in the whole data set of 1985 and 1986 (769 observations with the male localized), and in the radio-tracking data on the four males in the study plot in 1987 (375 observations). The figures are as follows:

	Foliage	Ground
1985+1986	88%	12%
Radio-tracking	65%	35%

(3) As the singing territories are stationary, one can be reasonably sure about the identity of singing males, i.e., mapping singing territories seems reliable although the birds were not individually marked. However, this is definitively not true of observations of silent males. There is no way of knowing that a silent male foraging within the limits of a singing territory is the territory holder. This is clear from our radio-tracking data (see Fig. 4A), but we have also obtained occasional visual records of colour-ringed males far outside their singing territories.

The point is that conclusions on territorial behaviour are circular if individual "territory-owners" are actually identified by their location!

(4) Identifying a "floating population" is more complicated than is often assumed; "non-stationary" males moving in other males' singing territories are not always floaters (see also Schartz & Zimmerman 1971). Removal experiments are necessary (e.g. Stewart & Aldrich 1951, Eckert & Weatherhead 1987).

(5) Radio-tracking makes it possible to monitor changes in the use of space by individual males through the breeding cycle. In this sense, our preliminary data are insufficient, and important further problems still exist in the variation in movement patterns over the season. Male-male aggressions are often more pronounced during territory acquisition and in the early phases of nesting than later on (e.g. Bergman 1953, Marler 1956b). Does this influence home range use as well? Also, how does breeding success influence the movement patterns of the males?

(6) The habitat structure or the local Chaffinch density may affect the movement patterns of the males. Male 5 (Fig. 4B), inhabiting a forest island surrounded by sapling stands, maintained a larger singing territory and moved in a larger area than males in the study plot. This difference may be due to the low Chaffinch density in the vicinity of the forest island.

Implications for Chaffinch territoriality

The dominant paradigm in theoretical studies of bird territoriality is to use "economic" models that assume food resource defence to be the determining factor of territorial behaviour (Brown 1964, Davies & Houston 1984, Carpenter 1987). However, such models are irrelevant for interpreting our Chaffinch data as the males foraged for long periods of time outside their singing territories, within the singing territories of neighbouring males (see also Zach & Falls 1979, Bédard & LaPointe 1984). In particular, geometric arguments concerning an optimal shape of the territory, relative to costs in seeking food resources and defending space (e.g. Hixon 1980, 1987, Schoener 1987), are suspect; the areas where the Chaffinch males actually foraged were not regular-shaped at all. We need critical assessments of the realism of the assumptions on which "economic" models are based.

Good descriptive data are needed on the territorial behaviour of different species for evaluating alternative hypotheses about the adaptive functions of bird territoriality (e.g. Hinde 1956, Marler 1956b, Brown 1969).

We need more data on how the birds actually use space once they have settled in a breeding site — this is a crucial problem in distinguishing between "singing territory" and "home range". How are different activities performed relative to the territory (foraging, fighting, copulations)? Several population studies include observations on territory owners using areas outside their territories (Lack 1939, von Haartman 1947, Marler 1956a, Snow 1956, Young 1956, Tompa 1964, Tryon & MacLean 1980, La Pointe & Bédard 1984, East & Hofer 1986), but the importance of this behaviour has usually not been assessed (but see Schartz & Zimmerman 1971, Zach & Falls 1979).

Also, the Chaffinch shows clear habitat preferences on the level of clearly discernible forest types such as coniferous, compared with deciduous forest (Bergman 1953, Glas 1960, Mikkonen 1985), but on the level of microhabitat variation in a mosaic-like landscape, such as our study plot, the relationships are less clear. It seems that different habitat elements corresponding to different requirements of the breeding pair (e.g. a safe nest site, singing posts, foraging areas) must be analyzed separately.

It seems that views on bird territories, adopted in the literature, are often typological, being based on assumptions that actually may not be realistic. This is the case if "territories" are defined by the position of nests (e.g. McLeery & Perrins 1985), or if "territory holders" are "recognized" by their location (e.g. Smith & Shugart 1987). If the distinction between territory and home range, suggested by our data, is more generally valid, such assumptions are circular.

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Selostus: **Pesivien peippojen laulureviirit ja elinpiirit tutkittuna visuaalisen havainnoinnin ja radiolähetintekniikan avulla**

Tutkimme peipon reviirin valintaa ja ympäristön käyttöä Seitsemisen kansallispuistossa vuosina 1985–87. Valitsemallamme 36 ha:n tutkimusalueella kartoitimme peippojen laulureviirit ja seurasimme värirengastettujen koiraiden liikkeitä alueella. Lintujen löytämisen ja seuraamisen helpottamiseksi otimme vuonna 1987 käyttöön radiolähettimet, jotka kiinnitettiin valjailla viiden koiraan selkään (kuva 2). Koiraista neljä oli tutkimusalueella ja yksi läheisessä taimikoiden ympäröimässä metsäsaarekkessa.

Kasvillisuus on laikuttainen koostuen pienialaisista vanhan metsän ja talousmetsän alueista, joita suot ja taimikot erottavat toisistaan. Puuston rakenteen kuvasimme aarin ruuduttain. Rakenteeltaan toisistaan selvästi eroavat laikut esitetään kuvassa 1.

Eri vuosina 11, 13 ja 13 peippokoirasta perusti reviirinsä tutkimusalueelle (kuva 3). Alueen vanhat ja kuusivaltaiset osat olivat joka vuonna "täynnä" peipporeviirejä, kun taas koillisosan mäntyvaltaiset osat harvemmin. Laulureviirit olivat tarkkarajaisia, mutta lisäksi koiraat liikkuivat hiljaisina laajalti laulureviirinsä ulkopuolella (kuva 4) ja viettivät jopa puolet ajastaan siellä (taulukko 1).

Optimaalista reviirin käyttöä käsittelevät mallit edellyttävät reviirin olevan tarkkarajainen alue, jossa kaikki linnun toiminnot tapahtuvat. Tuloksiemme mukaan olettamukset eivät ole peipon osalta realistisia.

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