

## Variation in territorial behaviour and breeding fates among male Chaffinches

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The territorial behaviour of male Chaffinches *Fringilla coelebs* was studied by radio tracking in coniferous forest in southern Finland. In total 24 males were tracked in 1988–90. The local Chaffinch population consisted of birds of different breeding status: most of the males were paired and started to breed, but some of them remained unpaired for the whole breeding season or remained unpaired after the disappearance of their mates. Nest predation increased asynchrony in breeding. The reaction to nest predation and the behaviour after successful fledging differed among both males and females. After fledging some males fed their young, whereas others did not participate in feeding but started to sing intensively. Some females made a new attempt at nesting whereas others disappeared, leaving their mates alone. The activities of the male Chaffinches were not restricted to the singing territory: all males made extra-territorial trips in every breeding stage. These trips were made for foraging or inconspicuously to the territories of other males, apparently in search of extra-pair copulations. Because of the asynchrony in the nesting cycles of different pairs, the local population included fertile females throughout the season, which increased the opportunities to pursue a mixed reproductive strategy.

### 1. Introduction

Recent studies have shown the importance of individual variation in behaviour within populations. Observed behavioural patterns are partly innate and partly dependent on earlier experience and events. The breeding strategy pursued by the male e.g., monogamy, polygamy (Alatalo et al. 1987) or a mixed reproductive strategy (Trivers 1972, Møller 1985, Birkhead et al. 1987) affects the territorial (Møller 1990) and singing behaviour (Temrin et al. 1984, Mace 1987, Møller 1988). The behaviour of individuals is the basis of behavioural studies and may explain ecological patterns or theoretical problems on a larger scale (Koehl 1989). The activities of

a territorial bird are not restricted to the territory. The males have been observed to make extra-territorial trips (von Haartman 1947, Marler 1956a, Tryon & MacLean 1980), though their function and frequency have seldom been determined (but see Scharz & Zimmerman 1971, Hanski & Haila 1988). Recently, the trips have been interpreted as intrusions into other territories to obtain extra-pair copulations (Birkhead 1987, Møller 1987) or as foraging movements (Williams 1990).

The probability that conflicts arise between different activities depends on the previous situations to which the individual has been subjected. For instance, after an unsuccessful breeding attempt the bird has to adapt to a new situation by

changing its behaviour or strategy. Female mortality usually causes nesting failure and the male can try to attract a new mate or to remain unmated and prepare for the moult and migration, possibly at the same time seeking copulations with other females. Nest predation causes a similar situation, but the decision of the male also depends on the reaction of the female, which either leaves or starts again with the same mate. After a successful fledging the male has two possibilities: either to help his mate to feed the fledglings and thus probably improve the survival of the young, or to let the female take care of the fledglings alone and to try to attract a new mate for a second brood (Harper 1985, Bart 1990).

The observations described in this paper have made us aware of the variability of territorial behaviour and space use in the individual life-histories of male Chaffinches *Fringilla coelebs* in southern Finland (Hanski & Haila 1988). The behaviour of a particular male at a particular time depends on his breeding stage and on the environmental factors encountered in the breeding season.

We present here a summary of our radio-tracking data on male Chaffinches in 1988–1990. We primarily want to demonstrate the variability in the breeding fates and behaviour of individual males, but also wish to relate our observations to theoretical questions of territory use and reproductive strategy.

## 2. Study area and methods

We collected our data by observing the behaviour of male Chaffinches by radio tracking in a 36 ha study plot in the Seitsemien National Park in southern Finland in 1988–1990. The study plot and its surroundings were conifer-dominated (mainly spruce) forests with a small proportion of deciduous trees. Forested areas were interrupted by small pine bogs and sapling stands. The methods and study area were described in Haila et al. (1987, 1989) and Hanski & Haila (1988).

The number of males monitored was 9, 5 and 10 in 1988, 1989 and 1990, respectively. In both 1988 and 1990 two males (males 5, 7, 15 and 21 in Appendix 1) inhabited two fragments of forest

(both about 1 ha) surrounded by sapling stands; the others frequented more uniform forest. We began to collect observations on each male two days after the radio tag was attached. Each observation period lasted one hour, but some shorter periods were included, mainly due to technical problems with the receiver in 1988. The tracking was mainly done in the morning (78% at 5–11 h and 22% at 12–19 h). We located the male with a radio receiver and then observed his behaviour by recording his spatial movements, time budget in territory use and interactions with females and other males. In 1989–1990 we also collected breeding data. The singing territories were defined by combining the outermost singing posts to form polygons. Our definitions of a singing territory area were based on over a hundred singing posts (median 153) per territory. The only exceptions were males 3, 6 and 7, whose singing territories were based on fewer (about 50) singing post records.

The observation periods did not cover the whole breeding season uniformly every year because of technical problems with the transmitters. In 1988 their individual duration was only 10–13 days, with only two transmitters functioning for a more adequate time of three weeks. In the following years the transmitters worked well, the duration being over 30 days. Signals were detectable up to 600 m in relatively flat terrain.

In 1989 we had problems with tag attachment. We used a similar harness in all years, including the pilot year 1987, as discussed in Hanski & Haila (1988), but in 1989 we made the neck loop of the harness rather too tight, and three males died because their beak had fastened under the string of the loop. In addition, three disappeared after tag attachment. A change in harness structure was made to prevent such accidents. We still think that the harness method is practicable for attaching the transmitter on a passerine of the size of the Chaffinch. The critical point is that the neck loop is large enough; thereafter with this provision the method worked as well as in the previous years (see Hanski & Haila 1988, Sykes et al. 1990). Each male was aged as one year old (1y) or more than one year old (+1y) according to the moult of the wing coverts (Svensson 1984), called “young” and “old” below.

### 3. Results

#### 3.1. Pairing status

Most of the males were paired, but a few seemed to remain unmated (Appendix 1). There also seemed to be a "floating population" of males that filled vacant sites and paired with vacant females, as shown by the replacements of the breeding males we accidentally removed in 1989. Among the radio-tracked birds, male 14 seemed to be a floater. He was captured in a mist net within another male's territory. He spent most of his time in an extensive area of sapling stands and drained bogs where there were no Chaffinch territories, from 50 to several hundred metres from the site of capture. He foraged and occasionally called but was heard singing only a couple of times.

Most of the breeding males were old (Appendix 1). In 1989, all except males 10 and 11 settled in their territories after the deaths of the previous owners, and these newcomers were perhaps previously non-territorial. Two breeding males disappeared in the middle of the breeding season, possibly because of predation, and in three cases the female left her male after nest predation, presumably as a reaction to an unsuccessful breeding.

#### 3.2. Territory settlement

The time when Finnish male Chaffinches acquire their territories is closely connected with melting of the snow cover on the breeding grounds (Bergman 1953, Mikkonen 1985). In springs with a late snow melt, male Chaffinches first settle in snow-free spots. Territory settlement occurred later in 1988 than in the other two years (Appendix 1). Only about one half of the males had settled on 5 May, when we started our field work. This seems to be connected with the exceptionally thick snow cover in 1988. On 5 May, the whole study plot was covered by a 30–40 cm thick snow layer, and about 50 per cent of the plot still had a continuous snow cover on 13 May. In other years the snow had melted and the males had already settled at the end of April. It should be noted that the radio-tagged males were not the only breeding males in our study plot.

In all years some males arrived later than others, and established their territories either by replacing the former territory owner, which moved to an adjacent area (two males), or by settling between other males and gradually enlarging their territories (one radio-tagged and two unringed males). The documented cases of replacement of territory owners occurred early in the breeding season in 1988. The boundaries of singing territories often moved between neighbouring males to the extent of about 20–40 m (Marler 1956b, Mikkonen 1985), or the territories expanded or contracted during the breeding season. The singing territories did not overlap at any point of time.

The number of Chaffinch territories in our study plot was 13, 10 and 22 in 1988–1990 (11, 13 and 13 in 1985–1987, see Hanski & Haila 1988). In 1989 the number was lowered by the deaths due to the tag attachment problems, and in 1990 the Chaffinch density was exceptionally high. In 1990 males also established territories in the surrounding low sapling areas, where there had never been territories during previous study years.

#### 3.3. Extra-territorial trips

The males regularly moved far outside their singing territories, spending 5–62% of the tracking time outside them (Fig. 1). Extra-territorial trips were conducted in all phases of the breeding cycle. In 1989 and 1990, when the breeding stages of the pairs were known, we calculated the proportions of time spent outside within each stage (Table 1). The mean proportions were fairly similar in different stages. However, males differed from each other: some males spent the greatest proportion of time outside during incubation, others during the nestling stage or when unpaired. The male-breeding stage interaction cannot be tested because too many of the data cells are empty (Table 1), due either to nest predation or to exhaustion of the tag battery. However, the proportion of time spent outside was not related to male age or breeding stage in any regular manner; there was no difference between young and old males (Mann-Whitney U-test,  $U = 141.5$ ,  $n_1 = 22$ ,  $n_2 = 15$ ,  $P = 0.477$ ) or among

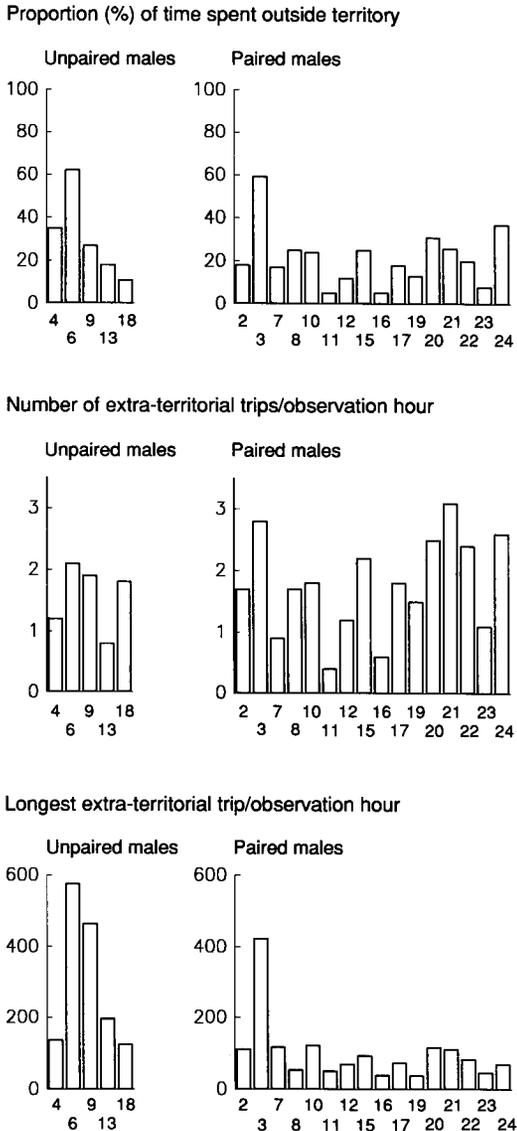


Fig. 1. Proportion (%) of time which males spent outside their territories, number of extra-territorial trips/observation hour and longest extra-territorial trip/observation hour of unpaired and paired male Chaffinches. The numbers on the horizontal axes indicate different males.

breeding stages (Kruskal-Wallis,  $H = 0.10$ ,  $df = 3$ ,  $P = 0.961$ ). During the pre-incubation stage several males made trips with their females up to one kilometre from their singing territory.

We used the longest extra-territorial trip in each observation hour to compare the movements

between males and breeding stages. Unmated males moved significantly farther away from their singing territories than paired males (Fig 1; Mann-Whitney U-test,  $U = 5.0$ ,  $n_1 = 5$ ,  $n_2 = 17$ ,  $P = 0.004$ ). The mean lengths of the longest trips in each observation hour were 98 vs 299 metres in paired and unpaired males (three years pooled). The same pattern was found in three males with sufficient tracking time in both paired condition and in the period when the males remained alone after disappearance of the female (male 15; 33 vs 123 m, male 20; 111 vs 142 m and male 21; 86 vs 218 m in paired and unpaired stages, respectively).

The trips were made both to territories of other males and to areas unoccupied by Chaffinch singing territories, in our study area mainly low sapling stands or forested bogs. During the three years we could determine the function of 88 trips. In 70 cases the male was foraging alone during his trip and in 18 cases the male was seen close to an obviously mate-guarding Chaffinch pair. In other cases the purpose of the trips remained obscure, but several purposes may of course be served by the same trip. Several males had favourite plots, to which they flew regularly for foraging on successive days. We recorded 16 such plots used by 13 males. In 1988 these plots mainly consisted of dense birch sapling stands or groups of old birches in the forest. This can be partly explained by a mass outbreak of birch aphids in southern Finland. The outbreak had a clear influence on the foraging behaviour of passerines, including the Chaffinch, and it may also have affected their foraging habitat preferences. In other years the Chaffinches also used other foraging areas on the ground, in forest or on bog.

### 3.4. Nesting success

The Chaffinches suffered heavy nesting failures due to predation on nests and probably also on adults. Three observations in this study and several in another area (Hanski 1992) indicate that most pairs make a new nesting attempt after nest failure. It seems that nesting failure is a factor responsible for the asynchrony in breeding within the population (Fig. 2, Appendix 1). In 1990 the nest of every radio-tagged male was found and

their breeding success recorded. We found nine nests, four of which were preyed upon and one deserted for an unknown reason (Fig. 2, Appendix 1).

In six cases in 1989–1990 in which the events after nest predation were recorded, three females disappeared after the nest failure and the males increased their singing. These female disappearances were not due to deaths, because in all cases the female was seen and heard making alarm calls near the nest soon after predation. Two of the cases in which the female left occurred moderately late (after 11 June) in the breeding season. In one case the male was observed to remate with a new female, but the success of the others remained unknown (year 1989 not shown in Fig. 2).

The events after fledging were known in four cases: two males fed their fledglings, moving outside their territories as well, and decreased their singing, but two males (17 and 23) did not feed their fledglings at all. Instead, they started

to sing actively within their singing territory. These two males were tracked for 7 and 8 days after fledging. In both cases the female was seen feeding fledged young, but the male did not take part in feeding. It is not known whether these two males remated or not. Male 16 disappeared in the midst of nest building, but the widowed female mated with a neighbouring unmated male and continued breeding in the same nest until it was preyed upon.

#### 4. Discussion and conclusions

The data described above revealed a great variation between the males in several aspects of behaviour. In comparisons made on larger geographic scale, density is an important factor. Chaffinch density was low in the Seitsemien area (in the coniferous forest about 50 pairs/km<sup>2</sup>) compared, for instance, with that in a lush spruce forest in Lammi in southern Finland (about 200

Table 1. Proportion of time (%) spent by males outside their singing territories in different breeding stages. Year 1988 omitted because breeding stages not exactly known. Highest proportion of time spent outside printed in bold face.

Male	Pre-inc.	Inc.	Nestl.	Fledg.	Unpaired
1989					
10	23	38	—	—	8
11	12	0	—	—	—
12	—	0	3	—	<b>24</b>
13	—	—	—	—	<b>18</b>
Mean	20	15	3	—	17
1990					
15	16	—	—	—	<b>32</b>
16	<b>17</b>	—	—	—	3
17	—	<b>23</b>	13	14	—
18	—	—	—	—	<b>11</b>
19	16	3	<b>19</b>	—	—
20	32	<b>54</b>	10	—	15
21	16	17	<b>61</b>	—	<b>38</b>
22	11	14	<b>33</b>	—	—
23	0	<b>12</b>	7	5	—
24	25	<b>52</b>	—	—	—
Mean	18	22	18	10	17

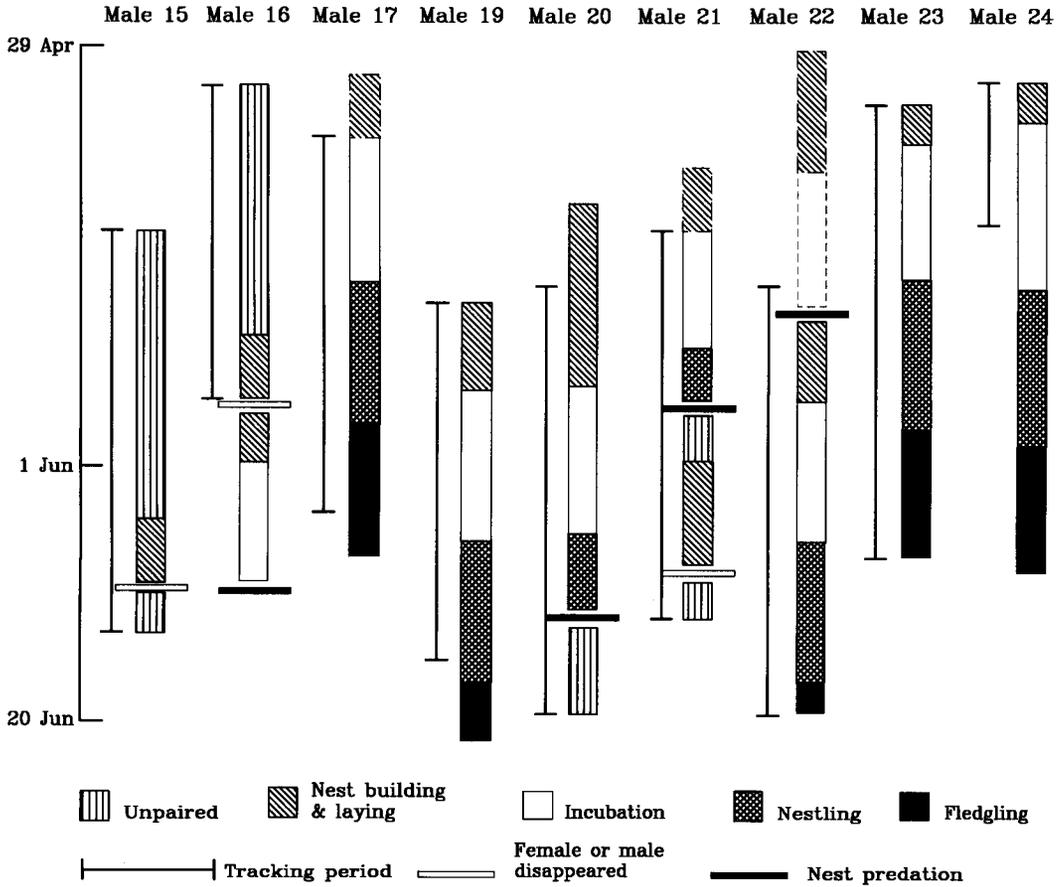


Fig. 2. Breeding data for the radio-tracked male Chaffinches in 1990. The ordinate gives the date. The parts of the columns outlined by dashes indicate the time for which exact dates are not known; the periods are then estimated from the mean duration of each breeding stage.

pairs/km<sup>2</sup> (see Hanski 1992). The Chaffinch territories were not tightly “packed” and the males seemed to be flexible concerning the boundaries of their singing territories, apparently depending on pressure from neighbouring territorial males.

Chaffinch males spent a considerable proportion of their time outside their singing territories both foraging and gathering food for nestlings. Thus, areas other than the singing territory are also important for foraging and during the nestling stage, when the amount of food resources may be most critical and the food within the territory is supposed to play an important role for nestlings (e.g. Stenger 1958, Schoener 1968, but see

Hinde 1956, La Pointe & Bédard 1984). Virtually every male gathered food for nestlings outside his singing territory (see also Hanski 1992). Males seemed to learn the location of resources outside their territories (see Williams 1990), because they returned to the same sites for foraging on successive days. It is highly improbable that this tendency to return to the same foraging sites is due to chance alone. Extra-territorial trips may thus help in locating distant food resources.

Defence of the singing territory may be advantageous during the fertile period of the female, that is, roughly 10 days before laying of the first egg until the day the penultimate egg is

laid (Birkhead et al. 1989). The singing territory acquired earlier in the breeding season may be a reasonably undisturbed area. However, mate guarding was not restricted to the singing territory; males followed females leaving the territory (see also Hanski 1992). Defence of the singing territory later in the breeding season is presumably advantageous, because if nesting fails, a new breeding attempt can be started immediately on the old territory.

Variation in the time of fertilization among females is increased by nesting failures (Brodsky 1988). High nest losses have been reported in the Chaffinch in other studies as well (Newton 1964, Payevsky & Vinogradova 1974). The new breeding attempts and asynchrony were not as prominent in Seitsemisen as in a high-density population in Lammi (Hanski 1992).

In an asynchronous population, males have a possibility of finding fertile females in their neighbourhood throughout the breeding season. In this situation it would pay for a male to pursue a mixed reproductive strategy: the male pairs and nests with one female but, in addition, tries to obtain extra-pair copulations (EPCs) and offspring with other females (Trivers 1972). This has recently been confirmed in several bird species (e.g. Birkhead 1979, Buitron 1983, Møller 1985, Alatalo et al. 1987, Westneat 1987, Newton 1989, Birkhead et al. 1990). The behaviour of male Chaffinches is consistent with the predictions of the mixed reproductive strategy (Hanski 1992).

We have no observations of extra-pair copulations, but this may be due to the difficulty of observing them. During the tracking in 1990 we observed 8 intra-pair copulations and 14 cases of an intruding male unobtrusively approaching a pair in the mate-guarding stage (see also Marler 1956a, Hanski 1992). In these situations the female was often in the copulation posture. The strange male approached so close to the female that fights occurred between the males or the mate-guarding pair moved away. These observations seemed to indicate deliberate attempts at EPC. The extra-territorial trips were found to be both foraging trips and partly inconspicuous trips to other territories. Thus, it seems that foraging, EPC-seeking and probably information-gathering are all functions of these trips.

After the death or disappearance of the female, the males usually started to make longer trips outside their singing territory and to sing more intensively within the territory. On the average, the males increased their singing 3–5-fold (this study, see also Hanski 1992, Hanski & Laurila, unpubl.). Increased singing may be interpreted as an attempt to attract a new female (Krebs et al. 1981, Sæther & Fonstad 1981), but it is not known whether the distant flights are performed to find a new mate, or in search of extra-pair copulations or a new territory.

Both Chaffinch males and females showed variable responses to nest predation and to successful fledging. The male's decision either to feed fledglings or to try to attract a new mate may depend on the stage of the breeding season (the young of our two males fledged early) and the number of fledglings in the brood (Westneat 1988, Byle 1990). The male whose young have fledged early would have time for a second brood, and if a brood consists of only a few young, the female may cope with feeding alone and the male can concentrate on a new breeding attempt. We also made three observations of the pair dividing their brood, the male feeding one part of the brood independently of the other part, which was cared for by the female (McLaughlin & Montgomerie 1985, Weatherhead & McRae 1990). However, more data are needed on such differences in individual behaviour before it is possible to assess their significance.

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## Selostus: Koiraspeippon reviiikäyt- täytymisen ja pesimämenestyksen vaihtelu

Tutkimme koiraspeippon reviiikäyttäytymistä Pohjois-Hämeessä Seitsemisen kansallispuistossa. Alueen maasto on pienipiirteistä erikäisten havumetsien ja soiden mosaiikkia. Tutkimuslinjan reviiireistä suurin osa sijaitti

kuusimetsävaltaisella 36 hehtaarin tutkimus-alueella. Lintujen havaittavuuden parantamiseksi käytimme apuna radiotelemetriaa. Seurasimme vuosina 1988–90 yhteensä 24 koiraspeippoa, mutta havaintojaksojen pituudet olivat hyvin vaihtelevia (Liite 1) johtuen radiolähettimien paristojen kestävyiden eroista.

Suurin osa koiraista pariutui ja aloitti pesinnän normaalisti, mutta populaatiossa oli myös reviiriä hallussapitäviä koiraita, jotka pysyivät parittomina koko pesimäkauden (Liite 1, Kuva 2). Pesäpredaatio lisäsi pesinnän epäsynkroniaa. Useimmat naaraat reagoivat pesäpredaatioon aloittamalla uuden pesintäyhteyden saman koiraan kanssa, mutta toiset katosivat reviiriltä, jolloin koiraat jäivät parittomiksi. Kaikissa tapauksissa, joissa naaras jätti reviirin, se nähtiin elossa vielä pesäpredaation jälkeen. Poikasten pesästälähtöön koiraat reagoivat kahdella tavalla. Osa koiraista ruokki poikasiaan, mutta toiset jättivät poikasten ruokinnan kokonaan naaraan huoleksi ja alkoivat sen sijaan laulaa innokkaasti, mahdollisesti houkutelakseen uuden naaraan toista pesyettä varten.

Kaikki koiraat liikkuivat kaikissa pesimävaiheissa laulureviirinsä ulkopuolella, joskin yksilöiden välinen vaihtelu oli suurta (Taul. 1, Kuva 1). Useimmiten koiraat lähtivät reviirin ulkopuolelle ruokailemaan, mutta usein myös vieraille reviireille, jolloin niiden käytös oli hyvin piilottelevaa. Tällöin koiraiden motiivina olivat ilmeisesti parisiteen ulkopuoliset parittelut. Tämä saattaa olla koiraille kannattavaa, sillä pesintöjen suuresta epäsynkroniasta johtuen populaatiossa on jatkuvasti fertiilejä naaraita.

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Appendix 1. Territory settlement, pairing status and breeding phase during radio-tracking period and breeding success of male Chaffinches. Status: U = unpaired, P = paired, PU = the male remained unpaired after disappearance of female, UP = the male was initially unpaired. Age: 1y = young, +1y = old. ST = singing territory, < = settled before that day.

Male	Age	Total tracking time (min)	Day of ST settlement	Status	Breeding phase	Fate of first nesting
1988						
1	1y	519	<5 May	U	pre-nest.	?
2	+1y	762	<5 May	P	pre-nest.-?	?
3	+1y	405	<5 May	P	pre-nest - nest build.	?
4	+1y	626	16 May	U	unmated	-
5	+1y	210	?	?	?	?
6	1y	318	5 May	U	unmated	-
7	+1y	275	?	P?	?	?
8	1y	569	<5 May	P	incubation	?
9	1y	811	3June	U	unmated	-
1989						
10	+1y	2306	<26April	P	pre-nest. -inc.	predation
11	1y	973	<26April	P	pre-nest. -inc.	failed
12	1y	700	24 May	P	inc.-nestl.	fem. died
13	1y	736	15 May	PU	unmated	-
14	1y	100	-	U	floater	-
1990						
15	+1y	1068	<5 May	UP	unmated-laying	deserted
16	1y	1151	<29April	UP	unmated-pre-nest.	predation
17	+1y	1501	<29April	P	inc.-fledgl.	fledglings
18	+1y	493	<29 April	U	unmated	-
19	+1y	1192	<29 April	P	pre-nest. -nestl.	fledglings
20	+1y	1509	<29 April	P	pre-nest. -nestl.	predation
21	1y	1232	<29 April	P	inc.-2. pre-nest.	predation
22	1y	1332	<29 April	P	pre-nest. -nestl.	failed
23	+1y	1487	<29 April	P	pre-nest. -fledgl.	fledglings
24	+1y	326	<29 April	P	pre-nest. -incub.	fledglings