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Flock formation, flock size and flock persistence in the Willow Tit *Parus montanus*

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The study was carried out in the alpine birch region in central Norway. According to flock attachment and behaviour juvenile Willow Tits were classified into five categories: regulars (permanent flock members), vanishers (flock members disappearing before New Year), irregulars (unsteady flock members), floaters and transients. Although the vanishers on the average arrived earlier in the area than the regulars and thereby, according to the current view, should benefit priority of being permanent flock members they nevertheless disappeared from the flocks after some time; the majority evidently emigrated from the area in October. It is suggested that the different behaviour of regulars and vanishers is hormonally based. The winter territories of flocks overlapped considerably. Flock size averaged initially 4.2 individuals (range 2–8 birds) and was composed of 2.3 adults and 2.0 juveniles. The sex ratio irrespective of age was 1.3, i.e. males outnumbered females. Thirty-two percent of the flocks contained more than 2 adults, some of which bred in the winter territory besides the dominant adult pair. Occasionally, even juvenile flock members bred successfully together with the adult pair within their common winter territory. Owing to strong fidelity, the birds usually kept to the same winter territory for life. Occasional territory (and flock) shifts were usually combined with pairing of individuals from different flocks, or divorces. Prior to establishment in winter flocks, the juveniles probably evaluate the resident pair and its habitat. It is furthermore suggested that juvenile flock members continuously try to improve their fitness, for example by frequently exploring areas outside their main territory, and that they are ready to change strategy if this seems beneficial.

1. Introduction

At least since the former century it has been well known that Willow Tits *Parus montanus* and its relatives congregate in flocks during winter (e.g., Collett 1864), although a more precise description of the composition and behaviour of such flocks were long in coming (e.g. Odum 1942, Haftorn 1944, 1956, 1990, 1997, Snow 1949, Hartley 1953, Dixon 1963, Smith 1967, 1988, 1989, Glase 1974, Ulfstrand 1975, 1977, Morse 1978, Hogstad 1978, 1987, 1989, Ekman 1979a, 1989a-b, Nilsson & Smith 1988, Nilsson 1988, With & Morrison 1990, Koivula 1994, Lens 1994, Lahti 1997, Silverin 1997). Typically, the Willow Tit winter flocks are dominance-structured (Hogstad 1987) and consist of one territorial adult pair and 2–6 non-kin juveniles, seldom more (e.g. Ekman 1979a, Hogstad 1987, Koivula 1994). The flocks are considered to be stable and coherent (Ekman 1979a, Hogstad 1987, Koivula & Orell 1988, Lahti 1997).

Despite an intensive study of Willow Tit flocks during the last few decades many questions still remain open. In fact, Silverin (1997) recently declared that "very little is known about the behaviour of postnatally dispersing juveniles and about how winter flocks are formed". Haftorn (1997, 1999) described postnatal dispersing of Willow Tit juveniles and presented some evidence suggesting that they assess the quality of territorial adults before settlement. The present paper provides further information about flock formation, their structure and stability.

According to the strength of flock association and duration of stay in the study area, juveniles were classified into five categories: (1) Regulars, i.e. permanent flock members still present in the study area after 1 January. (2) Vanishers, i.e. birds which initially became ordinary flock members (regulars), but disappeared before 1 January mainly due to switching to other flocks, emigration or death. (3) Irregulars, i.e. birds which were only loosely attached to a flock, implying that they did not occur in the flock as regularly as the other members. (4) Floaters (sensu Smith 1991), i.e. birds not being connected to any special flock, instead switching between several flocks or roaming about singly. Some individuals seemed to be in a transitional stage between (3) and (4). The grouping of birds in irregulars and floaters was therefore somewhat arbitrary. (5) Transients, i.e. birds which just passed through the study area, or stayed in the area for a few days only.

It is considered crucial for a juvenile Willow Tit to become a flock member (implying a reduced predation risk, increased winter survival, enhancement of finding food; e.g. Krebs et al. 1972, Ekman et al. 1981, Hogstad 1988a). Because chances of being incorporated in a flock decrease very rapidly with time (Koivula et al. 1993) an early settlement is important for the juveniles (Silverin 1997), enhancing their probability to find a vacant territory in an optimal habitat (Koivula 1994). Furthermore, an early settlement enables the yearlings to build up larger stores before the winter (Ekman 1979a).

The following suggestions were made. (1) Immigrating yearlings that become regular flock members arrive earlier in the territory than other juveniles. (2) Vanishers are mainly subordinates recruited from late arriving immigrants. (3) Irregulars and floaters involve mainly immigrants that arrive relatively late. (4) Transients are immigrants that arrive later in the study area than the former classes. (5) Since prior occupancy (seniority) seems important for obtaining a high social rank (Hogstad 1987, Nilsson 1988) yearlings should prefer to join resident adults while they still are alone. (6) Because Willow Tits are sedentary and highly site tenacious (e.g. Ekman 1979a, Koivula 1994, own data) flocks are expected to be stable over years apart from replacement of disappearing birds. Furthermore, according to the findings elsewhere in Fennoscandia (e.g. Ekman 1979a, Hogstad 1987, Koivula & Orell 1988), I expected that winter flocks entail less than 10 individuals, including the territorial adult pair, and that flocks contain seldom more than two adults each.

2. Material and methods

This study covers the period 1987–1996 and is part of a longterm project at Venabu (61°39´N, 10°08´E) in Ringebu municipality in central Norway. The study area (about 370 ha) is situated in the alpine birch region about 900 m above sea-level. The forest consists of *Betula pubescens*, intermingled with some coniferous trees (mainly *Picea abies*, a few *Pinus sylvestris*). *Juniperus communis* is patchily distributed all over the area. The type of forest is primarily heat birch forest with *Empetrum hermaphroditum* and *Vaccinium myrtillus* as dominants in the field layer. Only small parts may be classified as meadow birch forest with a more luxuriant field layer.

The only breeding tit species is the Willow Tit *Parus montanus*, except for a few Great Tits *P. major*, which sometimes join the Willow Tits in winter. Coal Tits *P. ater* on migration regularly pass the area in autumn.

Nearly all Willow Tits within the study area were captured, sexed, measured and colour-ringed. Juveniles with a wing length below 63 mm were considered to be females, those with wing length above 65 to be males. Juveniles with wing length in the area of sexual overlap (63–65 mm), but with a body mass below 11.0 g were determined to be females and those with a body mass above 12.3 g to be males (for further details, see

Haftorn 1997). Some birds could be sexed according to behaviour. Yet, the sex of quite a few birds remained unknown. Visible subcutaneous fat content in the furculum was scored according to a 4-level scale (0 = no fat, 1 = a little fat, 2 = about half-full, 3 = full). The birds were trapped at ten feeders scattered over the study area. These were baited with sunflower seeds during my visits, but not in the intervening periods. Trapping started in July–August and went on for a period of about one week each month (except for December and January in some years) until the next breeding season.

Only a few yearlings were recruited from the local population (most nestlings had been colour-ringed), i.e. the majority was immigrants to the study area.

During periods with heavy snow layer it was nearly impossible for me to penetrate the dense birch forest. I was then obliged to observe the birds along ski trails and at the feeders.

To identify all members constituting a winter flock is not an easy task and may require observations during several days and sometimes weeks. Birds belonging to the same flock often break up into subunits for periods of varying length, and birds observed together at feeding tables may belong to more than one flock. Furthermore, ambient temperature influences the coherence of flock members which tend to split into subunits during periods of relatively warm weather (Hogstad 1988b, Lens 1994).

Concerning statistical treatment of data it should be mentioned that data from different years are not quite independent, because some individuals are found in the same flocks in two or more years.

Rotten birch stumps useful for excavation of nest holes are in excess all over the study area. It is therefore unlikely that shortness of appropriate nesting sites plays any role in population regulation.

In a few cases pairs divorced. Only cases in which the mates part company after completed breeding (whether successfully or not) and establish new relationships while the original partners still are alive are accepted as examples of genuine divorces.

No field experiments were carried out during the study. Thus, except for artificial feeding during short periods and handling during ringing the population was practically undisturbed. All statistical tests were 2-tailed.

3. Results

3.1. Winter territories

The winter territories of flocks were not entirely exclusive. Due to considerable overlap even approximate borders between the winter territories were hard to determine, although each flock claimed a main area. Observations clearly showed that the birds frequently undertook prospective raids hundreds of meters outside their main territory and thereby discovered and utilized feeding tables in neighbouring territories (Haftorn unpubl.). It is unlikely that food provisioning influenced the size of the main territories seriously because the feeding tables were baited only periodically (see Methods). Thirteen flocks shared each year an area of approximately 250 ha of the total study area, giving on the average 19 ha to each flock. However, because of great overlaps each flock covered a much larger area, probably 20–30 ha.

3.2. Flock size

Flock size averaged 4.2 ± 1.43SD individuals (median 4, N = 101), varying between 2 and 8 individuals (Fig. 1). In this data set floaters were omitted. Yearly means fluctuated between 3.0 ± 1.04 and 5.2 ± 1.48 individuals (Fig. 2). Difference between years was highly significant (one-way ANOVA, $F_{9,100}$, $P < 0.001$. Flock size was rather low the first year (1987), but then increased significantly the next three years to a maximum of 4.8 individuals in 1990. This period was followed by two 3-year periods with a similar pattern of a within-period increase. However, a Spearman rank correlation analysis revealed no overall trend during the entire period ($r_s = 0.47$, $P > 0.05$).

The mean flock size in each of 13 winter territories spread over the study area varied from 3.5 ± 2.12SD to 5.0 ± 0.71 individuals. However, a Kruskall-Wallis test gave no significant differences among the territories ($P > 0.05$).

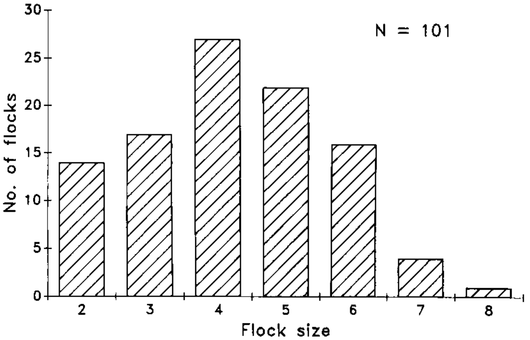

Fig. 1. The initial number of Willow Tits in winter flocks. Floaters excluded.

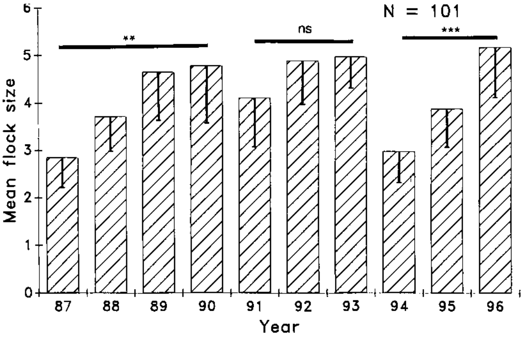

Fig. 2. Yearly mean size (with lower 95% confidence limit) of Willow Tit flocks in the period 1987–96. Floaters excluded. ** = P < 0.01, *** = P < 0.001, ns = not significant.

3.3. Flock composition

On the average the flocks (N = 101) consisted of 2.3 ± 0.99SD adults and 2.0 ± 1.39 juveniles, varying from 0 to 5 individuals in both categories (Fig. 3). The difference was not significant (Mann-Whitney U-test, z = – 1.572, P > 0.05). There was a significant, although weak, negative correlation between the number of adults and juveniles ($r_s = -0.31$, $P < 0.002$, N = 101). Juveniles were entirely lacking in 19% of the flocks. These flocks contained 2–4 adults (mean 2.6 ± 0.83SD, N = 19). As many as 32% of the flocks contained more than 2 adults (3–5). Omitting the year 1994 when juveniles were extremely scarce, the proportion of flocks without juveniles dropped to 9%. The maximum number of adults of known sex in a flock was 3 for both sexes.

Fig. 4 reveals mean number of juveniles and adults in the flocks over the years. Clearly, the extreme low number of juveniles integrated in flocks in 1994 accounted for the relatively small flocks this year (cf Fig. 2).

The background of flocks with more than two adults was rather complex. In some cases the "extra" adults had joined the flock as juveniles in a previous season, others became flock members as adults.

3.4. Sex ratio

Considering only flocks (N = 68) with individuals of known sex irrespective of age, the mean number of males in a flock was 2.1 ± 0.86SD and of females 1.7 ± 0.70, yielding a sex ratio of 1.3. Hence, there were more males than females in the flocks ($\chi^2 = 3.71$, P = approx. 0.05). Looking at juveniles and adults separately, a similar trend is found. For juveniles the mean number of males and females was 0.9 ± 0.93 and 0.6 ± 0.65 respectively, a significant difference ($\chi^2 = 4.75$, $P < 0.05$, N = 68 flocks). For adults the corresponding values were 1.2 ± 0.63 and 1.0 ± 0.52, although not significantly different ($\chi^2 = 1.49$, $P > 0.05$, N = 98 flocks). Figs. 5–6 reveal the distribution of young and adult birds of known sex in the flocks.

In flocks with an even number of members the sex ratio was mostly 1.0 (24 of 39 flocks), indicating that many birds had joined the flock in pairs. In 5 of these flocks there were "superfluous" individuals, viz. 2–4 extra males in 4 flocks and 2 extra females in one.

Looking at flocks with an odd number of members (N = 29), one "superfluous" male was found in 22 flocks, 2 males in one and 3 males in another, in contrast to only 5 flocks with a "superfluous" female, again indicating a male-biased sex-ratio.

3.5. The arrival time of immigrating juveniles

The date of capture (ringing) was used as approximate arrival time for immigrating juveniles. There was no significant difference between the estimated arrival times of males and females for any of the four categories of yearlings: regulars, vanishers, irregulars and transients (Mann-Whitney

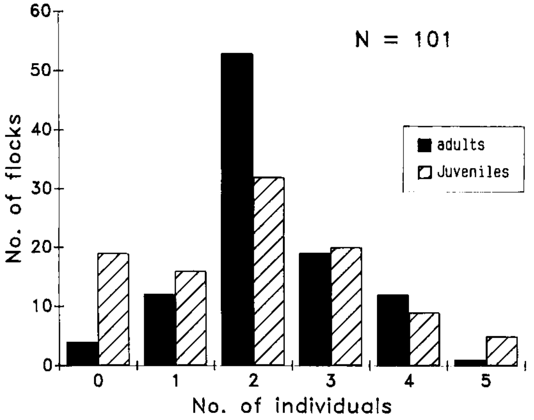

Fig. 3. Number of Willow Tit flocks with a varying number of adults and juveniles. Floaters excluded.

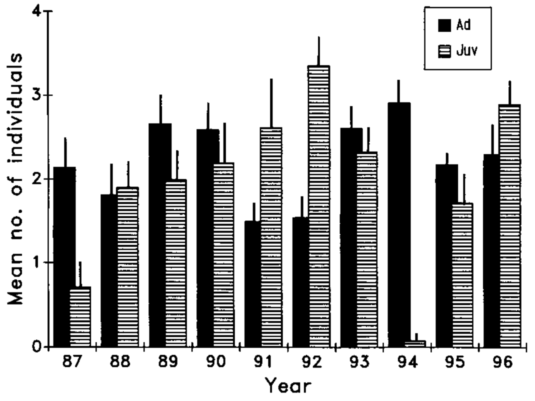

Fig. 4. Yearly mean (± 1 SE) number of Willow Tit adults and juveniles in the flocks during the period 1987–96. Floaters excluded.

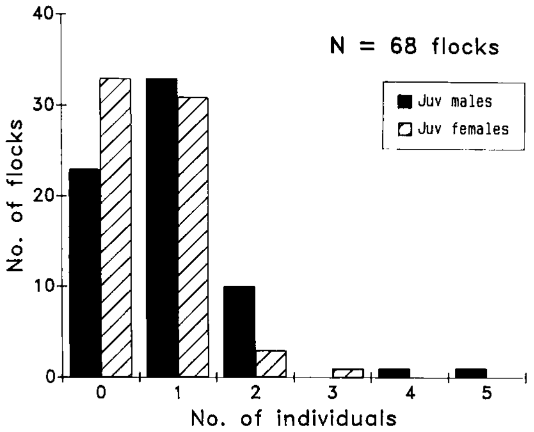

Fig. 5. Number of Willow Tit flocks with a varying number of juvenile males and females respectively. Floaters excluded.

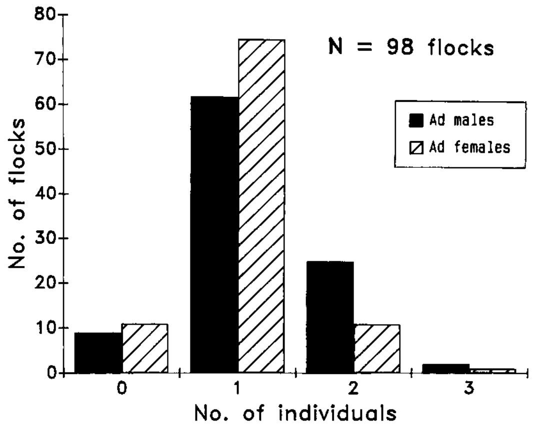

Fig. 6. Number of Willow Tit flocks with a varying number of adult males and females respectively. Floaters excluded.

U-test, $P > 0.05$). The data of the sexes were therefore lumped, resulting in the following mean arrival dates for immigrants during the first four weeks of the study (21 July–18 August): regulars 10 August ± 7.28SD ($N = 37$), vanishers 5 August ± 8.31 ($N = 35$), irregulars 9 August ± 6.19 ($N = 26$) and transients 8 August ± 6.45 ($N = 14$). One-way ANOVA gave $F_{3,108} = 2.78$ ($P = 0.04$), i.e. a significant difference between means. Additional t-tests showed significant differences between regulars and vanishers ($P = 0.01$) and between vanishers and irregulars ($P = 0.04$); however, with Bonferroni corrections these differences became insignificant ($P > 0.05$).

A consideration of the total immigration period (July–October), produced the following mean arrival times for the same classes: (1) regulars 6 September, (2) vanishers 20 August, (3) irregulars 30 August and (4) transients 12 September (Table 1). One-way ANOVA ($F_{3,313} = 11.65$, $P < 0.001$) showed a highly significant difference between the means. Additional Bonferroni tests verified significant differences between regulars and vanishers ($P < 0.001$), between vanishers and transients ($P < 0.001$) and between irregulars and transients ($P = 0.02$). Even when years were treated separately these differences did partly hold in Sign-tests. Thus, vanishers arrived on the average

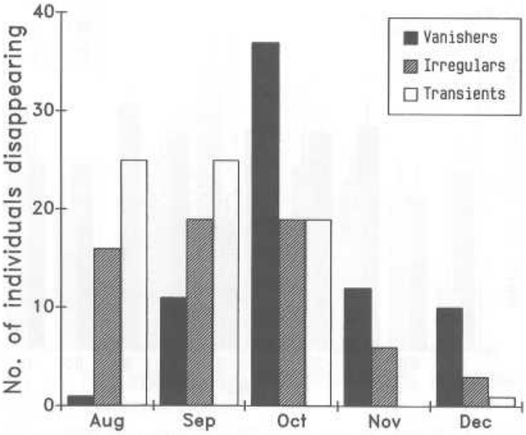

Fig. 7. Willow Tits disappearing from the study area before 1 January.

earlier than the regulars in 7 out of 8 years ($P = 0.07$), vanishers earlier than transients in 8 out of 8 years ($P < 0.01$) and irregulars earlier than transients in 6 out of 8 years ($P > 0.05$).

3.6. Time spent in flocks by vanishers, irregulars and transients

Of 212 juvenile regulars (106 males, 67 females, 39 of unknown sex) as many as 72 or 34% (36 males, 19 females, 17 of unknown sex) became vanishers and disappeared from the flocks before 1 January of the following year. Three birds died from accidents, 6 performed flock switching and one male that was a member of a 6-flock since the beginning of August became a floater in October. All the remaining birds just disappeared before January and were never recovered. October was by far the month during which most vanishers disappeared (Fig. 7).

At the time of their disappearance the vanishers had spent on the average 62 days in their respective flocks (Table 1).

Of 63 irregulars (26 males, 12 females, 25 of unknown sex) 50 or 79% (21 males, 11 females, 18 of unknown sex) disappeared before January. Their loose flock alliance lasted on the average 25 days, i.e. a significantly shorter period than for the vanishers (Table 1; one-way ANOVA, $F_{2,141} = 87.56$, $P < 0.001$; Bonferroni test for difference between irregulars and vanishers, $P < 0.001$). Only ten irregulars were observed after December, eight of which had moved to another locality within the study area. Twenty-six transients stayed in the study area for only 2 days on the average, significantly shorter than the vanishers and irregulars (Table 1; Bonferroni tests $P < 0.001$). Neither of the three classes showed any significant intersex differences (Mann-Whitney U-test, ns).

3.7. Social rank order and physical condition of vanishers and irregulars

The rank order of vanishers varied extensively. Twenty-two birds (11 males, 7 females, 4 of unknown sex) were all low-ranking flock members. In contrast, 13 males and 1 female possessed a relatively high social status and dominated at the time of their disappearance at least one another flock member, as exemplified by the following two birds. One male dominated all others in a 6-flock consisting of five juvenile males and one adult female. Having spent two months in the flock he nevertheless disappeared in October simultaneously with three other males and left behind the adult female together with a male which originally ranked number three in the hierarchy (these two became a pair which bred the following

Table 1. Mean (± SD) arrival time and mean (± SD) time spent in the study area for juveniles of different categories (for definitions, see text). In brackets range and number of records. * = $P < 0.05$, *** = $P < 0.001$, ns = not significant.

	Regulars		Vanishers		Irregulars		Transients		Floaters
Arrival time	6 Sep ± 25 days (23 Jul–21 Oct, 128)	***	20 Aug ± 22 days (21 Jul–23 Oct, 62)	ns	30 Aug ± 22 days (24 Jul–23 Oct, 60)	*	12 Sep ± 25 days (28 Jul–21 Oct, 69)	ns	14 Sep ± 37 days (5 Aug–20 Oct, 8)
Staying period(days)			62 ± 25 (10–123, 68)	***	25 ± 22 (2–91, 50)	***	2 ± 1 (1–5, 26)		

spring). Another juvenile male ranked second in a 5-flock which in addition to himself contained the adult alpha-male and his adult mate together with two juvenile females. Having joined the flock for more than one month the young male suddenly left the flock in late September and was not seen again until March the next year together with other Willow Tits at some distance from the original flock.

Physical condition in terms of wing length, body mass and fat score did not clearly separate the different classes including transients and floaters (Table 2), although female vanishers had slightly shorter wings than the regulars (one-way ANOVA, $F_{4,106} = 3.69$, $P < 0.01$; Bonferroni test for difference between regulars and vanishers, $P = 0.01$).

3.8. Characteristics of floaters

Some birds adopted the strategy of floaters, i.e. they ranged among several flocks or stayed alone. In all, 24 birds ringed as juveniles (12 males, 11 females, 1 of unknown sex) were assigned to this category. Nineteen of these were floaters during their first year of life, one throughout life (4 years) and the remaining four became floaters during their second or subsequent winter. Three birds being floaters as juveniles settled for breeding the following year and two more birds at a later stage. In contrast, three birds became floaters during the winter after breeding at the age of one year (at least two of them raised young successfully).

3.9. Transients

Many immigrating juveniles hardly stopped in my study area, and disappeared shortly after their arrival in August–October (Fig. 7). On the average, they spent only 2 days in the area (Table 1). Altogether 70 juveniles (19 males, 25 females, 26 of unknown sex) were classified as transients.

3.10. Winter flocks in relation to breeding performances

As mentioned above, many flocks contained more than two adults (3–5). The following spring the dominant pair (formed by two adults or the dominant adult male and a one year old female) settled to breed within the winter territory, using the same restricted area year after year. But what about the "extra" adults? Some of them simply disappeared at the end of the winter season, others (9 cases) established a breeding territory within or just outside the winter territory. If an appropriate mate was lacking within the flock (4 cases) the "extra" adults paired with unmated birds (in 3 cases with juveniles) from neighbouring flocks. Noteworthy, the dominant resident pair usually settled centrally in the winter territory, the subdominant pair more peripherally, 300–700 m apart (Mean 531 ± 194 m, N = 8). In one case a surviving adult female and a one year old male from the same flock both paired with birds outside the flock. The mutual rank of the two pairs was unclear and they both bred in the central part of the winter territory, 250 m apart

Table 2. Means (±SD) of wing length, body mass, fat score and time of capture (daytime hour) for different groups of juveniles. One-way ANOVA and Bonferroni tests were used to check differences between means. Number of records in brackets. ** = $P < 0.01$, ns = not significant

	Regulars		Vanishers		Irregulars		Transients		Floaters
Male									
Wing (mm)	65.5 ± 1.38 (69)	ns	65.5 ± 1.14 (36)	ns	65.9 ± 1.31 (27)	ns	65.6 ± 0.90 (19)	ns	66.2 ± 0.76 (5)
Body mass (g)	12.1 ± 0.62 (68)	ns	12.3 ± 0.41 (35)	ns	12.4 ± 0.64 (27)	ns	12.2 ± 0.43 (19)	ns	11.9 ± 0.51 (5)
Fat score	0.9 ± 0.58 (68)	ns	0.8 ± 0.58 (36)	ns	1.1 ± 0.57 (24)	ns	1.0 ± 0.93 (19)	ns	1.3 ± 0.89 (5)
Time	11.5 ± 3.17 (69)	ns	11.3 ± 3.15 (36)	ns	12.0 ± 2.75 (27)	ns	12.4 ± 3.72 (19)	ns	9.8 ± 2.50 (4)
Female									
Wing (mm)	62.8 ± 1.12 (48)	**	61.8 ± 0.85 (19)	ns	61.8 ± 0.83 (13)	ns	62.1 ± 1.23 (25)	ns	62.4 ± 1.21 (7)
Body mass (g)	11.2 ± 0.42 (47)	ns	11.1 ± 0.47 (19)	ns	11.3 ± 0.78 (13)	ns	11.1 ± 0.60 (25)	ns	11.2 ± 0.63 (7)
Fat score	0.8 ± 0.74 (47)	ns	1.0 ± 0.68 (18)	ns	0.9 ± 0.65 (12)	ns	0.9 ± 0.46 (25)	ns	1.0 ± 1.01 (7)
Time	11.0 ± 2.81 (48)	ns	10.7 ± 3.75 (19)	ns	11.5 ± 3.73 (13)	ns	11.0 ± 3.19 (24)	ns	10.7 ± 2.94 (6)

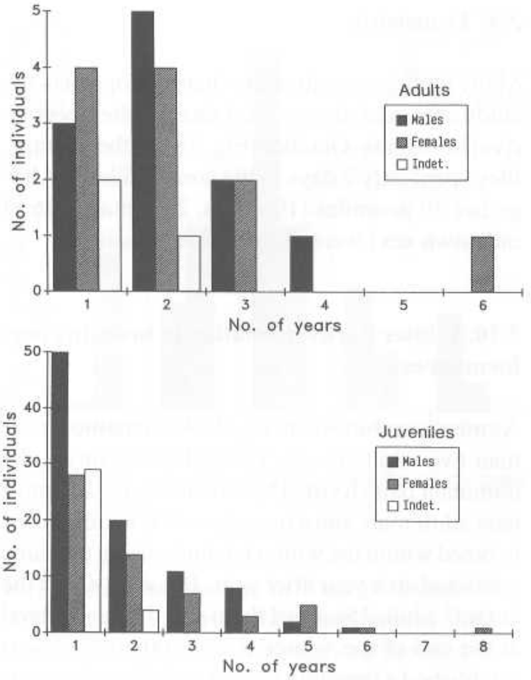

Fig. 8. Number of years juvenile and adult Willow Tits spent in flocks in their respective winter territories. Floaters exluded. Indet. = indeterminate.

from each other.

In 6 cases even juvenile flock members bred within or just outside the main winter territory of their respective flocks, 100–800 m apart from the old territorial pair (mean 433 ± 271 m, N = 6). In only one of these cases the juveniles forming the breeding pair both came from the same flock, in the remaining cases the juvenile flock member (4 males, 1 female) mated with a juvenile or in one case with an adult female from other flocks.

Although the dominant pair claimed a breeding territory centrally in the winter range, there was no evidence indicating that other breeding territories within the same area was of a suboptimal character.

No more than two breeding pairs derived from the very same winter flock. However, in two cases a third pair from other flocks managed to establish a breeding territory between the two former (at least 200 m apart from the others).

Once a pair had bred, the birds clearly tended to build their future nests very close to the first one, all often a few metres apart provided access to rotten stumps suitable for excavation.

When the summer was over the surviving members of the two pairs having bred in the same winter territory usually reunited, thereby restoring flocks with more than two adults. Pairs formed by birds from neighbouring flocks either went back to their former flocks after reproduction or joined the local flock.

In general, breeding pairs usually came from the same winter flock. This feature applied to 62 of 80 breeding pairs; in 12 cases the mates belonged to neighbouring flocks, in 3 cases to flocks with one territory in-between, in 2 cases to flocks with two territories in-between and in the remaining 2 cases the origin of one member was unknown. Having completed breeding, surviving mates nearly always joined the same winter flock (66 of 69 pairs). One pair derived from different flocks parted company after having bred successfully and went back to their former winter territories. Two other cases with exactly the same scenario were attributed to divorce and polygamy respectively.

3.11. Flock persistence, flock switching

Although the winter flocks disintegrated each early spring, surviving individuals clearly tended to associate with the same birds the following autumn. Thus, owing to strong fidelity, the birds usually kept to the same winter range for life. Very few birds survived more than 5–6 winters, however (Fig. 8).

Figs. 9–11 show the composition including shift of individuals in three different flocks during the years 1987–96. In one of the flocks there was a complete turnover after 4 years (Fig. 10).

Despite strong fidelity some birds nevertheless change territories during the winter and stay in that new territory for the rest of their life. Thus, breeding pairs formed by mates from different flocks require that one partner shifts territory (18 cases). The young male *lbab* offers a typical example. He belonged (winter 1991–92) to a 4-flock which in addition to himself consisted of one adult pair and a young female that probably was his "fiancé". The latter disappeared, however, around New Year, and on 28 February *lbab* moved two territories away and joined a flock originally containing one adult female, a young male and a

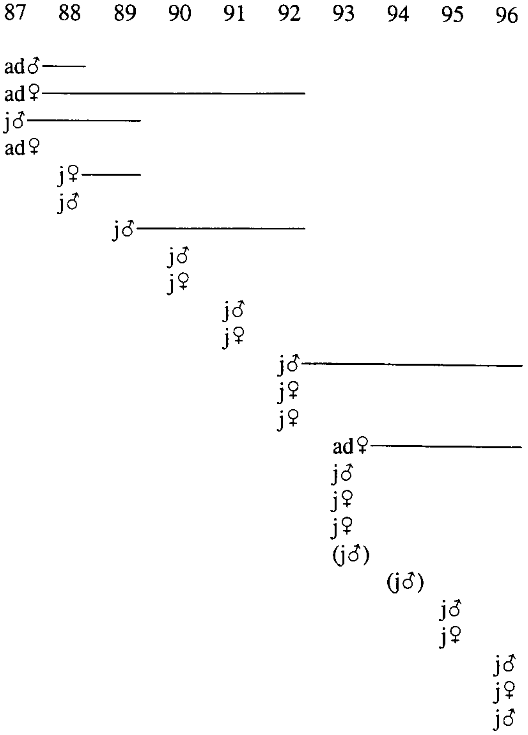

Fig. 9. The composition of the Willow Tit flock at winter territory A during the period 1987–96. Horizontal lines denote time spent in the flock. Explanation: at start the flock contained 4 individuals of which 3 survived until the next winter (1988–89) when the flock consisted of 5 individuals including 2 juveniles. Of the original flock only the adult female survived until the winter 1992–93 (was last seen 1 February 1993). Ad = adult, j = juvenile, ( ) = Floater, 87 = winter half year 1987–88, and so on.

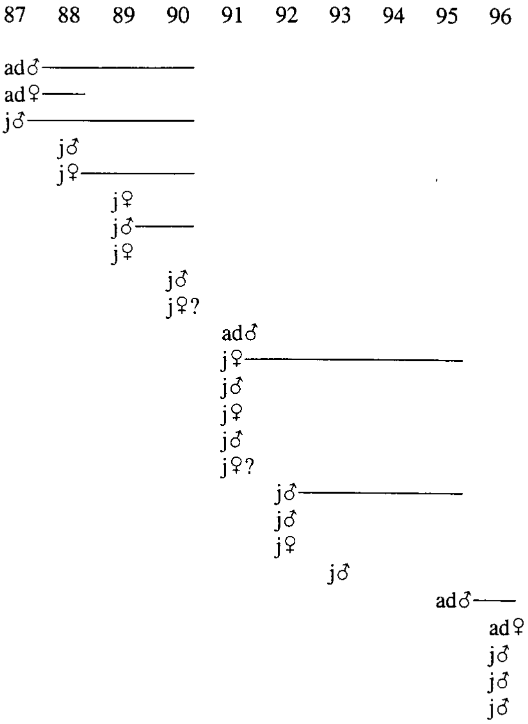

Fig. 10. The composition of the Willow Tit flock at winter territory B during the period 1987–96. At start of the winter 1991–92 the flock contained 6 individuals of which all were new. Ad = adult, j = juvenile, j♀? = sex uncertain.

young female. The young male vanished in December–January, whereupon *lbab* filled his place, mated the old female and was faithful to this territory until February 1995 when he vanished.

Divorces (7 cases) did also commonly lead to territory shift by one of the mates. Interestingly, divorces may be postponed until late winter or spring, implying that the birds spent the greater part of the winter together.

4. Discussion

The Willow Tit flocks claimed separate winter territories, although with great overlaps. Well-defined limits of the territories did therefore not exist, apparently in contrast to the situation in southern Sweden where Ekman (1979a) found a zone of overlap of only about 20 m. At the other extreme, in Canada flocks of Black-capped Chickadees *Parus atricapillus* did not occupy exclusive or defended areas (Desrochers & Hannon 1989). However, this result could have been due to the feeding regime (continuous provisioning of sunflower seeds; Desrochers et al. 1988).

The Swedish winter territories were huge, around 25 ha (Ekman 1979a, Ekman & Askenmo 1984). The Venabu territories were probably of about the same size when accounting for the overlaps. At Venabu, at least subunits of each flock made regular prospective trips far outside the main territory, thereby being faced with a wealth of information from the environment over a wide area, some of it being of vital importance to survival and future reproduction (e.g. food resources, habitat quality, mating and breeding possibilities, current composition of neighbouring flocks, den-

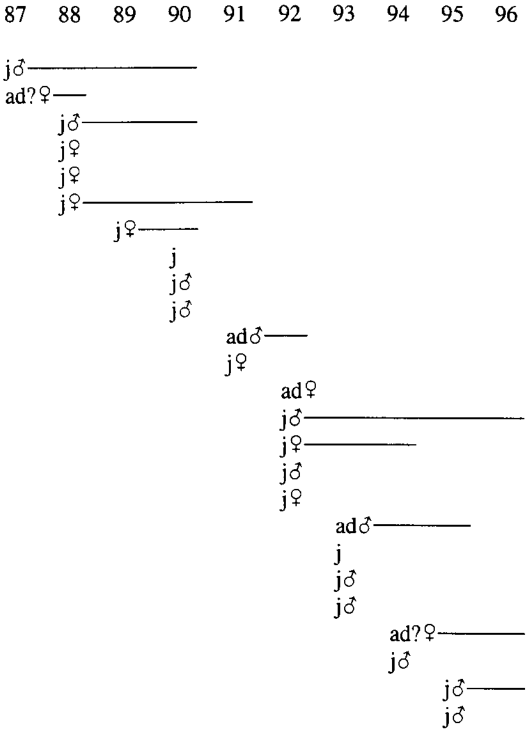

Fig. 11. The composition of the Willow Tit flock at winter territory C during the period 1987–96. Ad = adult, j = juvenile, ad? ♀ = age uncertain.

sity of conspecifics). This pattern became evident already in the beginning of the present study (Haftorn 1990). Interestingly, Ekman (1979a) did also observe single individuals outside their flock territories in winter.

The mean flock size of 4.2 Willow Tits in the alpine birch forest at Venabu was fairly similar to that found in coniferous forests in southern Sweden (4.1; Ekman 1979a), Norrbotten in northern Sweden (3.7; Alatalo & Carlson 1987) and northern Finland (4.6 and 4.9; Koivula 1994, Lahti 1997). At all places the most common flock size was four individuals, typically 2 adults and 2 yearlings. In similarity with the situation elsewhere in Fennoscandia the initial flock size at Venabu varied between 2 and 8 individuals.

In the subalpine mixed forest in Budal in central Norway, the mean flock size was somewhat higher, since almost all flocks consisted of 6 individuals in the beginning of the winter (Hogstad 1984). Hogstad (1987) suggested that the difference between 6 individuals in Budal in Norway and 4 in southern Sweden (Ekman 1979a) was caused by the absence of other tit species in Budal. However, this view was not supported by the findings at Oulu in Finland (Lahti et al. 1996) and Venabu (this study), where the small flock size was not associated with other species.

Why the flocks in two Norwegian alpine forests lying only 140 km apart differ significantly in size is most likely due to differences in habitat quality (carrying capacity). The study area in Budal is covered with an equal proportion of coniferous and birch trees (Hogstad pers. comm.), while the forest at Venabu is dominated by birch, probably making the latter inferior with regard to food supply. At any rate, it is no reason to believe that the Venabu flocks were incomplete due to lack of recruits, as suggested by Smith (1991), because the area each autumn was invaded by an excess of individuals. Furthermore, asymmetry in heterospecific competition is unlikely, since the Willow Tits at both sites live in single-species flocks. Nor does the scanty evidence so far warrant the conclusion that flock size in Europe increases with latitude (see Ekman 1989b). Whether the predation pressure distinguish the two areas is uncertain. Although they have the predominant predators in common (*Mustela erminea, M. nivalis, Martes martes, Aegolius funereus, Glaucidium passerinum)*, little is known about their relative abundance. It is unlikely that difference in feeding regimes between Budal and Venabu could have accounted for the different flock sizes, because the feeding tables at both sites were baited with sunflower seeds only periodically (see Methods).

On the average, flocks at Venabu contained an equal number of adults and juveniles. There was nevertheless a weak negative correlation between the two age groups (fewer juveniles with an increasing number of adults), lending support to the hypothesis that number of individuals is a main factor in regulation of flock size. Settling first year birds apparently avoid large social flocks (Ekman 1979a).

In the autumn, males outnumbered females in initial flocks, even when yearlings and adults were treated separately. Ekman (1979a) found the same tendency in the beginning of the breeding season.

The suggestion that mixed-age flocks at Venabu normally contain only 2 adults (the resident breeding pair) in agreement with the general findings elsewhere in Fennoscandia (Ekman 1979a, Hogstad 1987, 1990, Ekman & Askenmo 1984, Koivula & Orell 1988), did not hold. As many as 32% of the Venabu flocks contained 3–5 adults. Exactly the same number of adults was found in one third of the flocks studied by Lahti et al. (1996) at Oulu in northern Finland. Many winter flocks of the Black-capped Chickadee do also contain more than two adults (Smith 1991).

Furthermore, it turned out that when the flocks broke up in spring, many of the "extra" adults in the Venabu flocks settled and bred in the vicinity of the dominant pair within their common winter territory, although usually more peripherally in the area.

Noteworthy, not only "extra" adults, but even some yearlings in mixed-age flocks managed to claim breeding territories within the winter territory they belonged to. However, regardless of age no more than two breeding pairs derived from the very same winter flock. Thus, the winter territories were apparently sufficiently large to allow more than one pair to breed in the area, in similarity with the situation at Oulu (Lahti 1997). In contrast, Ekman (1979a) and Hogstad (1987) suggested that the only possibility for a juvenile Willow Tit to obtain a territory of its own is to wait until the resident adults disappear. In autumn, the territories in southern Sweden were claimed by small flocks, but many members disappeared up to the next spring, leaving within most territories, at the most, one breeding pair (Ekman 1979a). So the number of pairs breeding within a common winter territory may be a matter of mortality and territory size.

Fidelity to the winter and breeding territory is high. Surviving individuals usually assemble in the same winter flocks year after year. Therefore, several years usually elapse until a complete turnover of individuals. Shift of winter flocks (including territories) nevertheless occur, usually caused by pairing of individuals from separate flocks, or divorces.

Among authors, it is generally accepted that it is important for a bird to obtain a high social status. A high status involves less predation risk, higher winter survival, prior access to food resources and better chances for replacement of lost mates (Ekman & Askenmo 1984, Hogstad 1988c, Koivula & Orell 1988). However, a prerequisite for attaining a high social status is an early establishment (Hogstad 1987, 1990, Nilsson 1988, Koivula 1994, Lahti 1997). I therefore expected that (1) juveniles that became regulars in the Venabu flocks were among the first immigrants to the area and (2) that they, if possible, would select a lone adult pair to gain seniority and consequently a high social status. However, I was faced with the fact that birds which eventually became vanishers, arrived on the average several days ahead of the regulars. As could be expected, transients arrived significantly later than the vanishers and irregulars. If lone adult pairs were favoured during the juveniles' settlement, I would expect that they joined the first the best adult resident pair they met with and thereby secured a high social status, without risking that other juveniles in the meantime occupied the "vacant" seat. However, direct observations showed that prospecting yearlings did not immediately join resident adults which they met, whether the adults were still alone or not (Haftorn 1999). This circumstance calls for an explanation. Flock establishment is obviously a serious matter having great impacts on the individual's future life including winter survival and reproduction. For the tits, therefore, an evaluation of the prevailing situation seems justified. Evidence suggests that juvenile Willow Tits are not in any great hurry to settle in permanent winter flocks and that they carefully assess the quality of the adults and their territory before taking a decision (Haftorn 1997, 1999). Flock association may therefore be a trade-off between early settlement and evaluation of the adults and their habitat. Hence, prior arrival is apparently not the only prime factor determining establishment.

It should be emphasized that at the time of flocking it was impossible to distinguish between regulars and vanishers, as both classes initially were accepted as ordinary flock members; only the progressive development of events made a distinction possible. The crucial question is therefore not why they all became flock members, but why so many of them disappeared and by definition became vanishers. At least the following factors may be relevant to the problem: low social rank, poor physical condition, switching to other flocks, emigration, mortality, genetic or hormonal characters.

Looking first at the social rank, it turns out that 22 out of 36 vanishers (both sexes) ranked low in the social hierarchy, while the remaining 14 (13 males, 1 female) enjoyed a high position in their respective flocks, indicating that social rank is at the most a contributory factor to their fate. The history of the juvenile male *alro-o* may illuminate the problem. He belonged to a 4-flock consisting of one adult female, two young males and a young female. Although he dominated all the others, including the mate of the adult female, he left the flock on 21 September and was last seen the very same day in a neighbouring territory.

Concerning body condition, there was no significant differences among the classes, so physical quality in terms of body size and fat content can hardly be a likely cause. Symptomatically, two young males being the largest of all Willow Tits (adults included) ringed in this study (wing length 68 and 68.5 mm, body mass 13.6 and 13.4 g) both became irregulars despite early arrival (August).

Only a few birds died with certainty in the course of the autumn. Likewise, relatively few birds were explicitly known to have switched to other flocks. However, an analysis of the temporal pattern of disappearance shows that by far the greatest number of vanishers disappeared in October (Fig. 7). Because environmental factors are not considered to be especially harmful to the tits at this time of year it is unlikely that this massive disappearance was attributed to mortality. Although Willow Tits are not well adapted for migration, mass movements of juveniles are observed almost every year in September–October at inland and coastland bird stations in Sweden and Finland (Linkola 1961, Hildén 1971, Ehrenroth 1973, Tiainen 1980, Silverin et al. 1989, Silverin 1997). In his Swedish study area, Ekman (1979b) did also connect the disappearance of non-territorial Willow Tits in September–October with the peak intensity of mass movements, and suggested that the vagrant life of single non-territorial Willow Tits in the forest is a precursor of such movements.

Thus, the temporal pattern of disappearing vanishers at Venabu coincides with marked eruptive movements of Willow Tits elsewhere. It seems therefore reasonable to conclude that the majority of Willow Tits that disappeared from Venabu winter flocks in October had emigrated from the area (only ten vanishers fledged in the study area, the rest outside and was consequently originally immigrants). The factors triggering this emigration are unknown. At any rate, I have no indications whatsoever that the birds were evicted from their winter flocks by flock mates. It therefore seems that they left the flocks unaffected by the flock mates. To what degree their behaviour is genetically or hormonally controlled needs further study. Silverin et al. (1989) found that migrating Willow Tits in late September had significantly higher plasma levels of corticosterone than territorial birds and therefore put forward the hypothesis that this hormone is involved in the initiation of the autumn migratory behaviour of the Willow Tit. It seems that my vanishers are largely identical with the migrants of Silverin et al. (1989) and my regulars with their territorial birds. The early arrival of the immigrating vanishers in my study area and their concentrated disappearance in October might therefore have a hormonal cause.

Willow Tits may become floaters in the nonbreeding season at any stage of life. Some birds were apparently floaters throughout life, others for shorter periods only. The species may even change strategy within the same season. Thus, two young birds were initially regulars until October and January respectively, and from then on floaters. Taking into account that even some regulars show floater tendencies it seems to exist a continuum of birds between two extremes, those being tightly attached to flocks at one end and those being genuine floaters at the other. Consequently it is not always easy to classify individuals. Irregulars fit well into this continuum.

The floater strategy was not related to age or sex and was occasionally adopted even by adults that had successfully bred. All floaters, irrespective of sex and age, seemed to be unpaired. In marked contrast to the my observations, Ekman et al. (1981) found that no Willow Tits survived the winter as floaters in their Swedish study area.

Juvenile floaters and transients arrived apparently too late to secure flock memberships, in default of “vacant” seats.

There was no sexual difference in arrival times for any of the five classes (regulars, vanishers, irregulars, floaters, transients).

5. Concluding remarks

5.1 The scenario of decision-making and the question of "stable" winter flocks

From the time of fledging to the end of the following winter juveniles pass a series of life phases which follow one another in orderly sequence: Two-three weeks after fledging the juveniles become independent and soon thereafter leave the natal territory voluntarily (not being evicted by the parents). At this stage their vocal repertoire is well developed and food storing has started. They rapidly associate with other non-kin juveniles and roam about in the forest regardless of boundaries between adult territories. This situation facilitates an early "engagement" among the birds (Ekman 1979a, Haftorn 1992, 1993, 1997). Most mixed-kin juvenile flocks disintegrate in the late summer, resulting in an increasing occurrence of juveniles in pairs or single. This phase coincides with frequent contacts with territorial adults, probably implying that the juveniles evaluate the quality of the adults and their territory before they make an ultimate decision to settle. Thus, the juveniles do not immediately associate with any adult pair (Haftorn 1999).

Even after flock establishment, juveniles seem to continue evaluating their current position, always ready to utilize chances of improved fitness. Such a strategy would explain (1) why the birds frequently explore areas far outside their main winter territory, (2) why some birds switch to other flocks and (3) why even relatively high-ranked birds sometimes leave their flocks.

This strategy implies that flocks are not rigidly stable. Rather, individuals expose a flexible attitude and are continuously open for alternative life-styles that might improve their survival chances and future reproduction. Even the floater strategy might be such an alternative. Already Odum (1942) characterized the chickadee as "a strong individualist", the statement of which just as well matches the Willow Tit.

Hence, from the time of parental independence and throughout the following winter and spring each individual Willow Tit must make a series of decisions of vital importance for future life, e.g. when to leave the parental territory, where to prospect, with whom to mate, where and with whom to settle, when to leave the winter flock, when to move to another flock or adopt the floater strategy. It is a main task for future research to clarify the underlying criteria for such a decision-making, in which the hormonal state should be taken into account. Silverin (1997) and Silverin et al. (1989) found that corticosterone implants induced dispersal in juvenile Willow Tits in early autumn (July–August) and that migrating juveniles in late September had higher plasma levels of corticosterone than territorial juveniles. On the other hand, corticosterone treatment in late autumn (18 October–15 November) did not make the juveniles leave their territories.

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Selostus: **Hömötiaisen talviparvien muodostuminen, parvikoko ja parvien pysyvyys keskinorjalaisessa populaatiossa**

Kirjoittaja tutki tunturikoivikoissa talvehtivien hömötiaisten parvia Keski-Norjan tutkimusalueilla. Yhteensä vuosien 1987–1996 aikana aineistoa kerättiin 101 parvesta. Keskimäärin 250 ha tutkimusalueella esiintyi 13 parvea, joiden osittain päällekkäisten elinpiirin koko vaihteli 20–30 ha välillä. Parvissa oli keskimäärin 4.2 lintua (kuvat 1 ja 2), 2.3 aikuista ja 2.0 nuorta lintua (kuva 3). Tutkittussa populaatiossa oli enemmän koiraita kuin naaraita lukusuhteessa 1.3:1 (kuvat 5 ja 6). Parveen kuulumisen ja myöhemmän selviytyvyyden mukaan nuoret linnut jaettiin viiteen luokkaan: pysyvät parven jäsenet (regulars), ennen vuoden vaihdetta hävinneet parven jäsenet(vanishers), epäsäännölliset parven jäsenet (irregulars), parveen kuulumattomat linnut (floaters) ja läpikulkijat (transients). Yli kolmannes parviin asettuneista nuorista linnuista lukeutui ennen vuoden vaihdetta hävinneisiin, ja keskimäärin ne viipyivät parvissa 62 vuorokautta (taulukko 1). Nykykäsityksen mukaan aikaisin syksyllä parveen liittyminen on edullista nuorille linnuille, koska parven jäsenyydestä on oletettavasti kilpailua yksilöiden välillä. Vastoin odotuksia ennen vuoden vaihdetta hävinneet linnut kuitenkin asettuivat parviin ennen parven pysyviä (yli vuodenvaihteen selvinneitä) jäseniä. Suurin osa näistä hävinneistä ilmeisimmin siirtyi tutkimusalueelta pois viimeistään lokakuussa (kuva 7). Kirjoittaja esittää, että parven pysyvien ja hävinneiden jäsenten käyttäytymisero olisi hormonaalisesti säädeltyä. Epäsäännöllisistä parven jäsenistä liki 80% hävisi ennen vuoden vaihdetta ja niiden parvessaoloaika kesti noin 25 vuorokautta. Läpikulkijat viipyivät tutkimusalueella vain keskimäärin 2 vuorokauden ajan. Paikkauskollisuudesta johtuen monet linnut asuivat koko elämänsä samalla talvireviirillä (kuvat 8–11). Joitakin siirtymisiä talvireviiriltä ja parvesta toiseen havaittiin useimmiten toisen parven jäsenen kanssa pariutumisen yhteydessä. Parvien muodostumisen aikaan nuoret linnut arvioivat paikalla olevien lintujen ja niiden reviirin laatua ennen asettumistaan talviparviin. Kirjoittaja päättelee, että nuoret linnut jatkuvasti pyrkivät parantamaan kelpoisuuttaan vierailemalla aika ajoin talvireviirinsä ja -parvensa ulkopuolella ja esimerkiksi tarkkailemalla avautuvia mahdollisuuksia vaihtaa parvea.

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