

Ecology and behaviour of winter floaters in a subalpine population of Willow Tits, *Poecile montanus*

Olav Hogstad

Norwegian University of Science and Technology, Section of Natural History, NO-7491
Trondheim, Norway. E-mail: olav.hogstad@ntnu.no

Received 2. May 2013, accepted 10. October 2013

Willow Tits *Poecile montanus* maintain yearlong territories defended by a male and female mated pair. Outside the breeding season the adult pair lives together with two to four unrelated first-year Willow Tits that have settled after a post-natal dispersal. Because the habitat of the species is largely saturated with dominant territory owners and the flock size is limited, many juveniles fail to become resident flock members. These non-territorial birds behave as migrants during autumn or stay in the area for a short time (transients) or live as floaters that switch among flocks or roam about singly. The floaters (51 colour-ringed) and transients (450 colour-ringed) did not differ physically or in their foraging behaviour, whereas birds of these groups were more vigilant and used less time for foraging than residents (114 colour-ringed). Floaters were socially dominated by residents and also maintained a poorer nutritional status. The mean wing length of males observed for the last time in November was significantly longer than that of those seen for the last time in September or October, whereas no such differences were found for body mass or nutritional status. The floaters moved around solitarily and crossed several Willow Tit territories (males 2–8 territories, females 2–5 territories; mean territory size ca 25 ha). Only three male floaters settled, one disappeared in December the same year, one was seen for the last time in March and one in April the following year.



1. Introduction

The behaviour of solitary non-territorial birds is difficult to study because of their typically secretive nature. Few studies have therefore been capable of monitoring such individuals, probably because they comprise a very small proportion of most populations. In the present paper I describe some traits of the floaters observed in a 25-year study of Willow Tits *Poecile montanus*.

Willow Tits are among the few north temperate passerines that maintain a yearlong defence of their territories. Most species defend only seasonal territories. The yearlong territories of Willow Tits

are mostly defended by a male and female mated pair that allows the birds to assess territory and mate quality throughout the entire year. Outside the breeding season the adult mated pair lives together with unrelated first-year Willow Tits that have settled after a post-natal dispersal. Because Willow Tits live in a closed system (Cohen 1971) and the habitat of the species is largely saturated with dominant territory owners (Hogstad 1999), there is a limit to the number of winter flocks an area can accommodate. As also the flock size apparently is limited, mainly to 4–6 birds (Hogstad 1989a), many juveniles fail to become flock members and behave as migrants during autumn (e.g.,

Ehrenroth 1973). Others stay in an area for a short time (transients) without being connected to any particular flock consisting of residents, whereas some live as floaters that switch among flocks or roam about singly (Hogstad 1990).

Whereas the ecology and behaviour of territorial Willow Tits during the nonbreeding season is well known (e.g., Ekman 1979, Hogstad 1987, Lahti 1997), information on the behaviour of solitary non-territorials is almost lacking (but see Hogstad 1990, 2003). Floaters are rare in Willow Tit populations (Ekman *et al.* 1981, Koivula & Orell 1988, Lahti *et al.* 1998) and it has been suggested that they suffer from very high mortality (Ekman *et al.* 1981).

Why do some non-territorial juveniles (floaters) choose to stay in an area, whereas others (transients) emigrate? Can these alternative strategies be explained by differences in morphology and physical condition of the birds?

This is an empirical study on the behaviour of individually marked Willow Tit floaters. The study describes (1) a comparison of the size and condition of floaters versus transients, and (2) shows some consequences of floating behaviour by describing (a) the foraging behaviour of floaters versus transients and residents, (b) the floater's nutritional status and behaviour versus residents, and (c) their period of time in the study area and success in becoming established as territorial flock members.

2. Material and methods

The study was carried out in a subalpine mixed forest composed of Scots Pine *Pinus sylvestris* and Downy Birch *Betula odorata* in Budal, in central Norway (ca 63°N) in 1986–2010. The birds were caught in feeder-traps during July–October (mainly September–October) within a 5-km² area (from 2001 reduced to 3.5 km²), colour-ringed and their sex determined by a combination of wing-length (maximum length) and body weight (to the nearest 0.2 g) measurements (Haftorn 1982, Hogstad 1987). The birds were aged as juveniles (born in the previous summer) or adults (born before the previous summer) by the shape and abrasion of tail feathers (Laaksonen & Lehtikoinen 1976). As morphometric variables I measured body mass

(morning weight until 12:00) with a Pesola spring-balance, generally with an accuracy of 0.2 g, and their wing length, which is often used as an indicator of body size (Hogstad 2011). Fat reserves of the birds were found by examining the visible subcutaneous fat content in the furculum of birds caught between 10:00 and 13:00. The fat content was scored according to a four-level scale (0 = no fat, 1 = a little fat, 2 = half-full, 3 = full).

All Willow Tits (non-territorial and territorial birds) analysed in this study were juveniles. The majority of the 501 banded non-territorials apparently passed through the study area, or stayed there for just a few days (transients, typically only on the date of ringing). Large scale autumn movements are typical in Willow Tits (e.g., Ehrenroth 1973). Individuals observed more than twice over at least one week were regarded as floaters (males = 34, females = 17).

To find out whether the birds within the three groups (transients, floaters, residents) lived under different nutritional regimes, I measured the breadth of the growth bars along the axis on a tail-feather plucked of birds caught in the second part of September. These growth bars provide a day-by-day record of the nutritional status of the birds: the wider the growth bars, the better the nutritional status (Grubb 1989). These “original” feathers (DGO) had grown during the nestling and fledgling periods. Six to 8 weeks later, I recaptured the birds (floaters and residents) and collected the induced feather (DGI) that the birds had regenerated. In Budal, the winter weather most often set in about mid-October. The growth bars on the induced feathers therefore were laid down under winter condition with snow cover and spells of cold. Because some of the birds were trap-shy or had disappeared, the sample size of recaptured birds (floaters 32, residents 53) was less than the number ringed (floaters 42, residents 65). Sample sizes vary because not all data were available for all individuals.

In addition to the banded floaters, I occasionally observed unbanded Willow Tits moving quietly within territories of banded birds. Those birds might have been either non-residents or unbanded residents from outside the study area that had left their territories temporarily (see Hogstad 1999) and so were not included in the study.

To study the foraging patterns of the birds, in-

Table 1. Mean (± 1 SD) of wing length (mm), body mass (g), fat score (visible subcutaneous fat content in the furculum, scale 0–3), and breadth (mm of 10 daily growth bars on the left outermost tail feather grown during the nestling and fledging periods, DGO) of male and female transients and floaters of juvenile Willow Tits. Figures in parentheses denote sample sizes. Differences between floaters and transients were examined with Mann–Whitney *U*-tests (*z*).

	Transients (<i>n</i>)	Mann–Whitney		Floaters (<i>n</i>)
		<i>z</i>	<i>p</i>	
Males				
Wing	65.7 \pm 0.8 (212)	–1.76	ns	65.9 \pm 0.8 (34)
Body mass	11.9 \pm 0.2 (6)	–1.45	ns	12.1 \pm 0.4 (28)
Fat score	0.7 \pm 0.5 (6)	–1.87	ns	1.1 \pm 0.5 (28)
DGO	2.41 \pm 0.01(8)	–0.78	ns	2.42 \pm 0.04 (29)
Females				
Wing	62.8 \pm 0.9 (238)	–0.69	ns	62.7 \pm 0.8 (17)
Body mass	10.7 \pm 0.3 (4)	–1.26	ns	10.9 \pm 0.28 (13)
Fat score	0.8 \pm 0.5 (4)	–0.47	ns	0.9 \pm 0.64 (13)
DGO	2.39 \pm 0.01 (3)	–0.70	ns	2.40 \pm 0.02(13)

dividuals were recorded when first observed in birch or pine trees. Because predation of tits has been found to vary with their foraging height (Ekman & Askenmo 1984), I noted whether they foraged into the upper or lower halves. Only one record was made per individual per tree and no more than five records were made of an individual per day. In total, 363 records were made (transients 63, floaters 186, residents 114) during October–November. Also their activities (foraging, vigilance and “other”) were studied. When foraging, a bird held the tip of its bill below eye level; when vigilant, the tip of its bill was raised to eye level or higher (see Lendrem 1983, Hogstad 1988). Vigilance and foraging were treated as mutually exclusive. The different activities were quantified by using a delayed time point technique (see Ekman 1987). Once an individual had been identified, I started an electronic metronome and recorded the activity of the bird five seconds later. Such a time delay appeared to be sufficient to avoid discovery bias by ensuring that the activity recorded had a chance of being different from the one at first sight (Bradley 1968, Ekman 1987).

To describe the behaviour of the floaters towards resident flock members and their movements between flocks, the flock composition and the approximate area of the winter territories of the flocks were determined. The size and composition of the territorial flocks were determined on the basis of coherence (Ekman 1979) among the ringed

birds, and the hierarchical social order of the individuals within each flock was determined by observing the outcomes (winners and losers) of agonistic encounters at feeders (Hogstad 1987). Each flock studied consisted of one adult mated pair (*M* = male, *F* = female) and one or two juvenile males (*m*₁ and *m*₂) and one or two juvenile females (*f*₁ and *f*₂). Also the juveniles were considered as pairs (*m*₁–*f*₁ and *m*₂–*f*₂; see Hogstad (1987), Haftorn (1999a). The invariable dominance rank of the flocks was: *M* > *m*₁ > *m*₂ > *F* > *f*₁ > *f*₂.

While most feeders were stationary, others were temporary (1–2 days) and placed at various locations within the study area. The amount of sunflower seeds in feeders was small, and it hardly affected the survival of the birds. To account for emigration from the study area, areas bordering the study site were carefully checked each year.

All statistical tests are two-tailed.

3. Results

3.1. The non-residents – transients and floaters

Of the 501 (246 males, 255 females) non-territorial Willow Tits recorded in the study area during the 25 years, transients comprised 90% and floaters 10%. The number of juvenile floaters recorded (34 males, 17 females) was low and varied yearly

Table 2. Average time (minutes, mean \pm 1 SD) used in birch and pine trees by solitary transients and floaters, and mostly paired residents of juvenile Willow Tits. Times were recorded to the nearest half minute. Figures in parentheses denote sample sizes. Differences among the groups are examined with Mann–Whitney U-tests.

	Transients	<i>z</i>	<i>p</i>	Floaters	<i>z</i>	<i>p</i>	Residents
Birch	0.7 \pm 0.3 (36)	−0.31	ns	0.7 \pm 0.3 (49)	−0.45	ns	0.8 \pm 0.6 (43)
Pine	1.9 \pm 1.1 (27)	−0.49	ns	2.1 \pm 1.2 (25)	−2.49	0.01	2.7 \pm 1.1 (71)

from none (8 years) to 7 (1 year), with a mean of 2.0 per year. If the only year (1988) with an unusually high number (seven) of floaters is omitted, the average number of floaters per year comes to 1.8. The proportion of males to females was 2:1 in floaters, but nearly equal (0.9:1) in transients.

The wing length, body mass, fat score, and the breadth of the daily growth bar on the tail feathers grown during the nestling and fledgling periods (DGO) of male and female floaters did not differ from that of the transients (Table 1). Thus, floaters apparently did not differ physically from the transient Willow Tits in the area.

3.2. Time use and foraging behaviour of transients, floaters and residents

Comparisons of time used per tree of transients, floaters and residents (mostly pairwise) under approximately the same conditions (e.g., time of day, ambient temperature) in October, revealed no differences among the three groups in use of birch trees (One-way ANOVA, $F_{2,127} = 0.79$, n.s., Table 2). When in pines, however, the groups varied (ANOVA $F_{2,114} = 5.33$, $p = 0.006$): the resident flock members stayed significantly longer in a tree (mean 2.7 min) than transients (mean 1.9 min) and floaters (mean 2.1 min; Mann–Whitney *U*-test, $p = 0.013$; Table 2). Although floaters stayed slightly longer than transients in pines, the difference was not significant. No significant differences were found between sexes in time used in trees within each of the three groups (Mann–Whitney *U*-test, $z = -1.83$ to -1.62 , n.s.).

The shorter time in pines for transients and floaters compared to that of residents led to faster movements of the first two bird types. The Willow Tits avoided open areas and long distances from cover, and their use of birch trees was mostly em-

Table 3. Percentage use of upper and lower halves of birch and pine trees by transients, floaters and residents of juvenile Willow Tits, and the percentage distribution of foraging and scanning observations. Figures in parentheses denote sample sizes.

		Transients	Floaters	Residents
Birch	Upper	97 (35)	100 (49)	95 (41)
	Lower	3 (1)	0	5 (2)
	Foraging	11 (4)	8 (4)	37 (16)
Pine	Scanning	89 (32)	92 (45)	63 (27)
	Upper	85 (23)	79 (108)	85 (60)
	Lower	15 (4)	21 (29)	15 (11)
	Foraging	44 (12)	43 (59)	66 (47)
	Scanning	56 (15)	57 (78)	34 (24)

ployed in movement over boggy landscapes with few pines.

The birds within the three groups did not differ in height use in birch or pine trees (Table 3; $\chi^2 = 1.3$ – 2.2 , $df = 2$, n.s.), but differed in the distribution

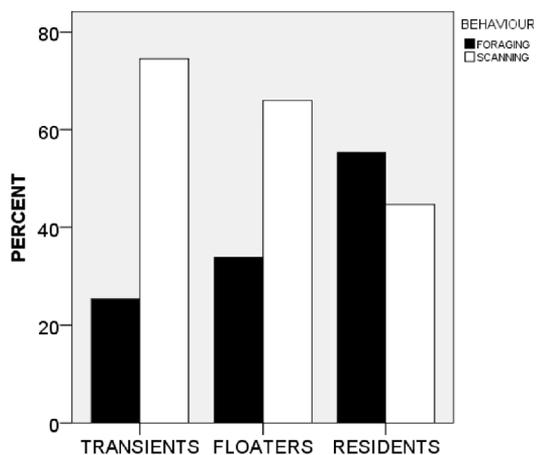


Fig. 1. Percent time used in foraging (black) and scanning (white) by transient, floater and resident juvenile Willow Tits when staying in birch and pine trees.

of foraging and scanning when staying in birch ($\chi^2 = 14.6$, $p = 0.001$) and pine trees ($\chi^2 = 10.4$, $p = 0.005$). Combining the data for bird's stay in birch and pine trees showed that transients (75%) and floaters (66%) scanned more than the residents (45%) which resulted in less time foraging for the non-residents than for the residents (Fig. 1; $\chi^2 = 19.61$, $df = 2$, $p < 0.001$). No significant difference in the distribution of foraging and scanning was found between transients and floaters ($\chi^2 = 1.56$, $df = 1$, n.s.) or between the sexes ($\chi^2 = 0.03$ – 3.26 , $df = 1$, n.s.).

Floaters stored sunflower seeds when alone at feeders. In the presence of residents, however, storing was nearly absent. I have no data on whether stored food was later eaten by the cacher.

3.3. Nutritional status of floaters and residents

Fat score did not differ between floaters and residents (Table 4), whereas the average daily growth bar width of the induced feathers (DGI) grown during October–November was significantly narrower in both male and female floaters compared with that of residents. Thus, even though floaters in the study area had the same fat score as the territorial residents, they apparently maintained a poorer nutritional status.

No difference in fat scores was found between sexes of either floaters or residents (Mann–Whitney U -test, $z = -1.79$ to -1.23 , n.s.). Likewise, the average daily growth bar width of the induced feathers (DGI) showed no sexual difference among floaters ($z = -1.79$, $p = 0.08$), but male residents scored higher (1.43, $n = 34$) than female residents (1.35, $n = 19$; $z = -4.80$, $p < 0.001$).

3.4. Behaviour of floaters versus flock members

Floaters behaved submissively when approaching residents. When attending a feeder, they mostly waited for the other birds to leave first or sought seeds on the ground. Confrontations were rare, probably because the floaters obviously avoided the more socially dominant residents. When a male resident approached, floaters withdrew or

Table 4. Average fat score (0–3) and breadth (mm) of the daily growth bars on induced tail feathers (DGI) plucked in October–November of male and female floater and resident juvenile Willow Tits. Figures in parentheses denote sample sizes. Differences between floaters and residents were examined with Mann–Whitney U -tests.

	Floaters (<i>n</i>)	Residents (<i>n</i>)	Mann–Whitney <i>U</i> -test	
			<i>z</i>	<i>p</i>
Males				
Fat score	1.1 (28)	1.1 (34)	–0.10	ns
DGI	1.24 (21)	1.43 (34)	–5.64	< 0.001
Females				
Fat Score	0.9 (13)	1.0 (25)	–0.88	ns
DGI	1.22 (11)	1.35 (19)	–3.43	< 0.001

were often observed to freeze with their head turned away from the threatening bird. This type of evasive posture was often observed (Fig. 2, right).

In addition to the general escape posture, male and female floaters behaved quite differently towards territorial residents: females occasionally approached a feeder with residents with wing-quivering, as if begging for food. This was observed 13 times in September and once in October. Males were never observed wing-quivering, but when taken by surprise by a resident at a feeder, they were observed executing a form of threatening behaviour with wings extended (Fig. 2, left) towards male residents (m_1 : $n = 4$; m_2 : $n = 7$) and female residents (f_1 : $n = 4$); all in September. In such cases the male residents responded by ignoring the “attacking” floater male that immediately withdrew. The female resident, however, approached the floater sometimes with its rump and back feathers fluffed, which resulted in the floater withdrawing. Only two supplanting attacks were observed: when a male resident (m_1) chased a male floater that foraged less than a meter from a female resident (f_1 , probably his mate), and when a male floater that stayed at a feeder was attacked by a male resident (m_2).

Some floaters were observed attending flocks for brief periods (1–2 days), but except for three males that replaced male residents that disappeared in November (see Floater success), they did not settle permanently. When accompanying residents away from feeders, they behaved inconspic-



Fig. 2. Three postures frequently used by interacting Willow Tits. Left: two threatening displays; upper, a high-ranked bird tilting its head upwards and exposing its black throat badge towards another individual. This display is silent and extremely brief (filmed and discovered when played back in slow motion). Lower, a bird fluffing of back feathers with wings dropped and held out from the body and tail spread. The bird at right shows an escape posture: it pull its head and body feathers in tight to the body and lean away from a higher-ranked bird. This escape display has a subduing effect on the aggressor and the bird usually avoids being attacked. The bird at left in the photograph is a dominant that exposes its black throat badge towards a subordinate which adopts the general escape posture.

uously and were rarely observed being chased or supplanted by residents.

In contrast to residents, floaters did not respond to playback of songs or calls.

3.5. Body size and fat reserves of floaters related to their time in the study area and area used

The mean wing length of male, but not female floaters, observed for the last time in November was larger than the wing length of those observed for the last time in September or October (Mann–Whitney, $z = -2.01$ and -2.35 , respectively, $p < 0.05$). No such differences among months were found for body mass, fat score or DGI (Table 5). Thus, males observed for the last time in Novem-

ber were larger than those observed for the last time in September or October, whereas physical condition seemed to be of less importance in determining how long floaters stayed in the area.

The floaters ranged over large areas: males over two to eight territories and females over two to five (Table 6). The mean number of territories visited by floaters increased with their time in the area. Thus, floaters observed for the last time in November ranged over more territories than those observed for the last time in September or October (Mann–Whitney U -test, $z = -3.04$ to -2.92 , $p = 0.003$ for males; September–November, $z = -2.00$, $p < 0.05$ for females). Although males were seen in slightly more territories than females in each of the months, the difference was not significant (monthly: $z = -1.77$ to -0.52 , n.s.; the total period: $z = -1.62$, n.s.).

Table 5. Body size, fat reserves and breadth (mm) of the daily growth bars (DGI) on tail feathers plucked in October–November of juvenile Willow Tit floaters observed for the last time in the area in September, October or November. Figures in parentheses denote sample sizes.

	September		October		November	
	Males	Females	Males	Females	Males	Females
Wing length	65.8 (7)	62.8 (4)	65.9 (21)	62.7 (12)	66.7 (6)	63.0 (1)
Body mass	12.1 (6)	10.8 (1)	12.0 (17)	11.0 (11)	12.4 (5)	10.8 (1)
Fat score	1.0 (6)	1.0 (1)	1.0 (17)	0.8 (11)	1.4 (5)	1.0 (1)
DGI	1.29 (3)	1.44 (1)	1.24 (14)	1.20 (10)	1.21 (4)	–

Table 6. Number of territories visited by male and female juvenile Willow Tit floaters seen for the last time in September, October or November. Figures in parentheses denote sample sizes. Differences between sexes were examined with Mann–Whitney *U*-tests.

	Males		Females		Mann–Whitney <i>U</i> -test	
	Min–max (<i>n</i>)	Mean ± SD	Min–max (<i>n</i>)	Mean ± SD	<i>z</i>	<i>p</i>
September	2–4 (7)	2.7 ± 0.8	2 (4)	2.0	–1.77	0.08
October	2–7 (21)	3.4 ± 1.2	2–4 (12)	3.1 ± 0.7	–0.44	0.66
November (*)	4–8 (6)	5.7 ± 1.5	5 (1)	5.0	–0.52	ns
Sept.–Nov.	2–8 (34)	3.7 ± 1.5	2–5 (17)	2.9 ± 0.9	1.62	0.11

(*) One of the males became a resident when he replaced a resident (m_2) that disappeared in November.

The movements of some floaters were rapid. In October two males moved nearly 2 km within two hours, i.e., they crossed 4–5 territories. Two male floaters transported and released approximately 1 and 1.5 km, respectively, outside the study area in October, were seen at their trapping places the next day. Although anecdotal, these observations indicate a familiarity with the area.

The floaters did not show any evidence of pair bonding. However, when near baited feeders two floaters occasionally were seen simultaneously. When attending the feeder, larger males (wing length) dominated smaller males (i.e., either caused the other to withdraw from the feeder or wait until the other bird left the feeder). Males always dominated females ($n = 5$).

3.6. Floater success

Although replacements occurred when a flock member disappeared, only three cases could be verified on the basis of colour-ringed juveniles categorized as floaters. One of the replacements was a male floater that replaced a resident male (m_2 in a flock of six) that was removed experimentally in November. The widowed female (f_2) accepted the male floater that was later frequently observed together with this female. They survived the winter, but both were seen for the last time the following March. On one occasion, when an adult alpha male (M) disappeared from its territory in November, the resident juvenile m_1 and his mate f_2 moved up in the dominance hierarchy and took the position as the alpha pair. The formally alpha female (F) disappeared. Then a floater attended the flock and became a low ranked m_2 . He survived the win-

ter without a mate and was observed for the last time the following April. When a resident male (m_1) was removed and held in captivity in November (he disappeared two days after the release), his mate (f_1) disappeared some days later. A male floater attended the flock for brief periods. His social status in the flock was unknown, and he disappeared in the second part of December of same year.

4. Discussion

4.1. Settlement decision

In many habitats there is an upper limit to the density of territories or social flocks. Thus, once all social units have been established, unestablished Willow Tits must decide whether to leave the area or try to settle within existing units. Unestablished individuals apparently are birds that arrive too late to get a position within a winter flock and thus are forced to become non-residents (Ekman *et al.* 1981, Hogstad 1990). Although these birds have access to the area, they are forced to accept a fitness loss relative to being a resident in a winter flock (e.g., Hogstad 1990). Juveniles that settled in less favourable habitats disappeared during the winter, suggests that this is not a viable option (Hogstad 1989b). Since membership in a winter flock may serve as a “ticket” to enter the habitat, selection obviously acts on parents to make their young able to disperse early, and on the young to reach potential establishment sites early (see Nilsson 1988).

The degree of territorial aggression by resident Willow Tits against attending non-residents may

vary, but previous studies have shown that the lowest ranked flock members constrained settlement decisions of floaters by aggressive behaviour (see Hogstad 1989b). Although floaters were observed attending flocks for brief periods, they did not settle permanently unless vacancies appeared (Ekman *et al.* 1981, Hogstad 1989b). The lack of replacements after November suggested that there were no floaters in the area during the winter. The same has been found earlier for Willow, Crested *Lophophanes cristatus* and Marsh Tits *Poecile palustris* (Ekman 1979, Ekman *et al.* 1981, Koivula & Orell 1988, Nilsson & Smith 1988, Hogstad 1989b).

Assuming that non-residents make up approximately half of the juvenile Willow Tits in the area (Hogstad unpublished), the number of floaters in the present study comprises about 5% of the juvenile part of the population. In northern Finland, Lahti *et al.* (1998) estimated the floater portion of Willow Tits to be about 1%. The ratio of males to females among the non-residents in the present study was 49:51. Among the floaters, however, the ratio was 66:33, i.e., a substantial excess of males. Haftorn (1999a) found that Willow Tit females were in excess among the non-residents. On the other hand, Orell *et al.* (1994) found that first-year male Willow Tits outnumbered females among the non-breeders.

The question why some of the unestablished Willow Tits choose to stay in the area as floaters while the majority emigrated is still unanswered. No significant differences were found between transients and floaters in size, physical condition or foraging behaviour. As the most severe bottleneck for juveniles is the difficulty in becoming established, advantages for floaters that stay in the area for longer times may include, in addition to heightened chances of gaining access to a winter flock, better knowledge of foraging areas, predator locations or escape cover. In sum, dispersal probably inflicts a cost through increased mortality.

4.2. Floaters versus residents

Since Willow Tits experience relatively high winter mortality (Ekman 1984), mostly because of predation (Jansson *et al.* 1981), they clearly have

to devote a great deal of time to surveillance. Solitary floaters do not benefit from cooperative sentinel behaviour as flock members do, and are therefore forced to invest more time in personal vigilance with a loss of foraging time as a result. Flocking allows the tits to economize vigilance time (Hogstad 1988), suggesting that a trade-off between foraging and predation is important in determining winter survival. As they are subordinate to residents, floaters also have an increased vigilance level when being close to residents. Even when only two resident juveniles were observed together, each bird used less time for scanning compared to that of single floaters. In addition, floaters stayed for shorter times in pines when foraging compared to residents, and thus moved more often than residents and so probably increased their detectability by predators (cf. Rajala *et al.* 2003). Willow Tits in flocks of only three members were found to have higher plasma levels of corticosterone (an important indicator of stress) than in flocks containing four or five birds (Silverin *et al.* 1984). This indicates that the increased time spent watching for predators influenced the birds negatively. The cost of watching for predators may be very large for individuals living singly. Other studies suggest that the adrenocortical response to social stress plays a key role in both the proximate and ultimate causes of floating behaviour (Brown & Long 2007).

Floaters were in poorer nutritional condition (DGI) than residents, presumably because of the costs of vigilance. However, the fat scores of floaters and residents did not differ. This argues against the optimal body mass hypothesis that predicts subordinate floaters, which have lower food predictability than residents, should have larger fat reserves (Lima 1986). However, results from a study of the same Willow Tit population showed a larger fat deposition of floaters compared to residents in the hours after 13:00 (Hogstad 2013), i.e., of birds checked later in the day than in the present study.

A floater strategy could be to maintain a restricted home range and get prior experience at a site to improve the chance of acquiring a territory in future years. In addition, it is likely that floaters maintain an advantage through a greater knowledge of the local food supplies, enabling them to attain a higher net rate of energy intake without incurring the cost of a higher predation risk. In the

present study, floaters moved over areas encompassing 2–8 territories. As the average territory size of Willow Tits is about 25 ha (Ekman 1979, Koivula & Orell 1988, Hogstad 1999), most floaters moved over large areas (about 100 ha), apparently to assess the quality and status of territories and flock members while seeking a vacancy in a flock. Haftorn (1999b) observed that a floater (sex unknown) moved among three different flocks until it eventually disappeared on 15th October of the same year.

Floaters that stayed in the area until November visited more territories than those that disappeared in September or October. Moreover, males, but not females, observed for the last time in November were larger than those seen for the last time in September or October. If there is a relationship between floater size and time enduring in the area, there may exist a form of hierarchical queue of birds waiting for an opening in a flock and that individuals maintain their rank in the queue by social dominance through interactions with other floaters.

Although juvenile residents regularly update their information about the composition and dominance structure of adjacent winter flocks by visiting them in attempt to become dominant owners during winter (Hogstad 1999), floaters may be more likely to detect potential vacancies because they move through the population rather than being restricted to one or a few territories.

When a flock member disappears, it is reasonable to expect that a lower-ranked member will form a pair with the widowed bird (Hogstad 1988). However, earlier findings from my Budal study area have shown that this is not always what happens. Since the residents apparently are paired, it seems that most residents are locked into their rank by their pair bond and do not form a pair with another bird in the same flock. Instead, they replace the widowed bird as a pair (Hogstad 1999). By contrast, floaters, which apparently do not form pairs while floating, are free to move in and insert into a flock. However, the chance of finding a vacancy in a flock before mid-winter seems small because of the low mortality of residents before January (Hogstad 1989b).

Probably the most common way a floater can establish in a winter flock is to persist in its attempts. The lost foraging time and the higher en-

ergy demands because of scanning and escape behaviour to dominant residents, however, may also lead to the need for solitary and undisturbed foraging. As the residents constrain settlement decisions of floaters, social interactions between residents and non-residents may be a factor in understanding the evolution of dispersal. Even though the odds are small, the floaters probably make the best of a bad situation and increase their chances of surviving the winter by staying in an area and thereby increasing the chances of inserting into a flock and subsequently entering the breeding population.

Acknowledgements. The manuscript was improved through valuable comments by T. C. Grubb, Jr.

Ekologi och beteende hos icke-etablerade solitära talltitor på vintern

Hos talltitan *Poecile montanus* försvarar hanar med make sitt revir året runt. Utanför häckningen håller paret ihop med 2–4 obesläktade ungfåglar, som efter en postnatal strövpriod bildar ”vinterflock” med paret. Eftersom gynnsamma områden har en hög täthet av dominanta revirhävande individer och flockstorleken är begränsad, blir inte alla ungfåglar medlemmar i sådana vinterflockar.

En studie från mellersta Norge 1986–2010 visade att största delen av ungfåglar som inte hörde till någon vinterflock flyttade ut från området, medan en mindre del (ca 10 %) blev kvar i området som icke-etablerade ”flytare”. Dessa dominerades – förutom av de revirhävande individerna – av de unga etablerade flockmedlemmarna. De var mer vigilanta, använde mera tid för födosök och hade sämre näringsstatus än unga fåglar som hörde till en flock. Vingen var i genomsnitt längre hos ”flytare” som sågs för sista gången i november, jämfört med de som sågs sista gången i september eller oktober, men ingen sådan skillnad hittades i kroppsvikt eller näringsstatus.

”Flytarna” var solitära och rörde sig över flera revir (hanar över 2–8 revir, honor över 2–5 revir; då man räknar med en revirstorlek på ca 25 ha). Av ”flytarna” blev endast tre hanar flockmedlemmar: en blev sedd i december samma år, en blev sedd sista gången i mars och en i april året efter.

References

- Bradley, J.V. 1968: Distribution-free Statistical Tests. — Prentice Hall, London.
- Brown, D.R. & Long, J.A. 2007: What is a winter floater? Causes, consequences, and implications for habitat selection. — *Condor* 109: 548–565.
- Cohen, J.E. 1971: Casual Groups of Monkeys and Man. — Harvard University Press, Cambridge.
- Ehrenroth, B. 1973: Studies on migratory movements of the Willow Tit *Parus montanus borealis* Selys-Longchamps. — *Ornis Scandinavica* 4: 87–96.
- Ekman, J. 1979: Coherence, composition and territories of winter social groups of the Willow Tit *Parus montanus* and the Crested Tit *P. cristatus*. — *Ornis Scandinavica* 10: 56–68.
- Ekman, J. 1984: Density-dependent seasonal mortality and population fluctuations of the temperate-zone Willow Tit (*Parus montanus*). — *Journal of Animal Ecology* 55: 119–134.
- Ekman, J. 1987: Exposure and time use in Willow Tit flocks; the costs of subordination. — *Animal Behaviour* 35: 445–452.
- Ekman, J. & Askenmo, C. 1984: Social rank and habitat use in willow tit groups. — *Animal Behaviour* 32: 508–514.
- Ekman, J., Cederholm, C. & Askenmo, C. 1981: Spacing and survival in winter groups of Willow Tit *Parus montanus* and Crested Tit *P. cristatus* – a removal study. — *Journal of Animal Ecology* 50: 1–9.
- Grubb, T.C. Jr. 1989: Ptilochronology: feather growth bars as indicators of nutritional status. — *Auk* 106: 314–320.
- Haftorn, S. 1982: Variation in body measurements of the Willow Tit *Parus montanus*, together with a method for sexing live birds and data on the degree of shrinkage in size after skinning. — *Fauna norvegica Ser. C, Cinclus* 5: 16–26.
- Haftorn, S. 1999a: Flock formation, flock size and flock persistence in the Willow Tit *Parus montanus*. — *Ornis Fennica* 76: 49–63.
- Haftorn, S. 1999b: Initial winter flock formation in the Willow Tit *Parus montanus*. Do immigrating juveniles assess the quality of territorial birds? — *Ibis* 141: 109–114.
- Hogstad, O. 1987: Social rank in winter flocks of Willow Tit *Parus montanus*. — *Ibis* 129: 1–9.
- Hogstad, O. 1988: Advantages of social foraging of Willow Tits *Parus montanus*. — *Ibis* 130: 275–283.
- Hogstad, O. 1989a: The role of juvenile Willow Tits, *Parus montanus*, in the regulation of winter flock size: an experimental study. — *Animal Behaviour* 38: 920–925.
- Hogstad, O. 1989b: Subordination in mixed-age bird flocks – a removal study. — *Ibis* 131: 128–134.
- Hogstad, O. 1990: Winter floaters in Willow Tits *Parus montanus*. A matter of choice or making the best of a bad situation? — In *Population Biology of Passerine Birds* (eds. Blondel, J. *et al.*): 415–421. Springer-Verlag, Berlin.
- Hogstad, O. 1999: Territory acquisition during winter by juvenile Willow Tits *Parus montanus*. — *Ibis* 141: 615–620.
- Hogstad, O. 2003: Strained energy budget of winter floaters in the Willow Tit as indicated by ptilochronology. — *Ibis* 145 (online): E19–E23.
- Hogstad, O. 2011: Wing length as a predictor of body size in the Willow Tit *Poecile montanus*. — *Ornis Norvegica* 34: 24–27.
- Hogstad, O. 2013: Fattening strategies and social status in Willow Tits *Poecile montanus* during the non-breeding season: support for the optimal body mass hypothesis. — *Transactions of the Royal Norwegian Society of Sciences and Letters* 2013: 1–13.
- Jansson, C., Ekman, J. & Brömssen, A. 1981: Winter mortality and food supply in tits (*Parus* spp.). — *Oikos* 37: 313–322.
- Koivula, K. & Orell, M. 1988: Social rank and winter survival in the Willow Tit *Parus montanus*. — *Ornis Fennica* 65: 114–120.
- Laaksonen, M. & Lehikoinen, E. 1976: Age determination of Willow and Crested Tit *Parus montanus* and *P. cristatus*. — *Ornis Fennica* 53: 9–14.
- Lahti, K. 1997: Social status and survival strategies in the Willow Tit *Parus montanus*. — PhD-thesis, Oulu, Finland.
- Lahti, K., Orell, M., Rytönen, S. & Koivula, K. 1998: Time and food dependence in Willow Tit winter survival. — *Ecology* 79: 2904–2916.
- Lendrem, D.W. 1983: Predation risk and vigilance in the Blue Tit (*Parus caeruleus*). — *Behaviour Ecology and Sociobiology* 14: 9–13.
- Lima, S. 1986: Predation risks and unpredictable feeding conditions: determinants of body mass in birds. — *Ecology* 67: 377–385.
- Nilsson, J.-Å. 1988: Causes and consequences of dispersal in Marsh Tits: time as a fitness factor in establishment. — PhD-thesis, Lund, Sweden.
- Nilsson, J.-Å. & Smith, H.G. 1988: Effects of dispersal date on winter flock establishment and social dominance in Marsh Tits *Parus palustris*. — *Journal of Animal Ecology* 57: 917–928.
- Orell, M., Rytönen, S. & Koivula, K. 1994: Causes of divorce in the monogamous Willow Tit, *Parus montanus*, and consequences for reproductive success. — *Animal Behaviour* 48: 1143–1154.
- Rajala, M., Ratti, O. & Suhonen, J. 2003: Age differences in the response of Willow Tits (*Parus montanus*) to conspecific alarm calls. — *Ethology* 109: 501–509.
- Silverin, B., Viebke, P.-A. & Westin, J. 1984: Plasma levels of luteinizing hormone and steroid hormones in free-living winter groups of Willow Tits (*Parus montanus*). — *Hormones and Behavior* 18: 367–379.