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Rank-related response in foraging site selection and vigilance behaviour of a small passerine to different winter weather conditions

Olav Hogstad

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

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The foraging patterns and time spent on vigilance behaviour by Willow Tits (*Poecile montanus*) were studied under varying weather conditions in a subalpine forest in central Norway during the winters of 2009–2013. The birds adjusted their microhabitat use in pines and their vigilance levels in response to perceived risk of predation and starvation. At low temperatures, the dominating adults foraged mainly in the upper and most predation safe areas in pines and the subordinate juveniles in the more predator risky lower halves. When the outer canopies of pines were covered by snow, the adults tended to restrict their foraging activities to the inner parts of the lower halves of the trees and thus overlapped considerably with the juveniles. In windy weather, the age classes differed in site use, mostly because juveniles foraged more in the outer part of the branches. Juveniles were significantly more vigilant than adults under all the weather conditions, and they spent about 60% of their time seeking food whereas adults spent about 85%. It is suggested that the high level of vigilance by the subordinate juveniles is costly and may be the main cause of the higher winter mortality of juveniles compared to that of adults.

1. Introduction

Weather conditions are an important factor for wintering small birds. Severe weather, like low ambient temperatures, high wind speeds or snow cover on trees, makes the birds vulnerable because they need to forage almost continuously during daylight to meet their energy demands (e.g., Wachob 1996, Cooper 2000). However, more time spent foraging entails lower vigilance and thus higher predation risk. Therefore, even though small birds frequently suffer from energy shortages (Jansson *et al*. 1981), they have to cut back on vigilance to acquire sufficient energy so as not to starve to death during the night. As energy stress is high on cold winter days, the birds are forced into a trade-off between vigilance and foraging. When they increase their vigilance, the birds have to reduce the time available for feeding and therefore increase the probability of starvation if foraging is unpredictable. Thus, predation may be an important agent determining the behaviour and niche use in birds (e.g., Villen-Perez *et al*. 2013).

The present study analyses data collected on foraging site use and vigilance behaviour in Willow Tits (*Poecile montanus*) of different social status during different weather conditions. Outside the breeding season, the birds, being only 10–12 g, live in flocks generally consisting of an adult territorial pair and two to four non-kin juveniles. With-

in each flock there exists a linear dominance hierarchy where adults dominate juveniles of the same sex, and within each age group males dominate females (Hogstad 1987). One of the main reasons why winter mortality among adults is lower than among low-ranking juveniles (Ekman 1984, Hogstad 1989a, Koivula *et al*. 1994) may be that dominant adults force lower ranking birds to use more exposed foraging sites, while selecting the safest spots for themselves (Ekman & Askenmo 1984, Hogstad 1988a).

Because high wind speeds or snow accumulated on tree surfaces have a negative impact on bird foraging behaviour by making the search for food more difficult (e.g., Brotons 1997), it may be suggested that the birds optimize their energy balance by changing their use of space as weather conditions change. Furthermore, because the segregation in foraging sites between dominant adults and subordinate juveniles is more marked in cold than in mild weather (Hogstad 1988b), I studied the vigilance behaviour of the birds at different temperature regimes.

The present study analyses data collected on foraging location use by Willow Tits in trees in winter in relation to their social status in the flock in different weather conditions, and whether time spent on vigilance is related to predator-safe sites and/or to flock size.

2. Material and methods

The field work was done from mid-November through February during 2009–2013 in a subalpine mixed forest composed of Scots Pine (*Pinus sylvestris*) and Downy Birch (*Betula odorata*) in Budal, in central Norway (c. 63°N). The wintery weather most often sets in about mid-October. The Budal woodland is characterized by a semi-continental and slightly oceanic climate. At this latitude, the daylight period is short in midwinter (21 December: 4 hrs. 31 min.). Potential predators of Willow Tits in the area are small mustelids such as Stout (*Mustela erminea*) and Weasel (*M. nivalis*), small owls such as Tengmalm's Owl (*Aegolius funereus*) and Hawk Owl (*Surnia ulula*) in twilight or at night, and Sparrowhawk (*Accipiter nisus*), Siberian Jay (*Perisoreus infaustus*) and Great Grey Shrike (*Lanius excubitor*) during the day. During the last decade, the Magpie (*Pica pica*) has been more numerous in the lower part of the study area.

Willow Tits were caught in feeder traps during July–October (mainly September–October) within a 3.5 km^2 area, individually colour ringed and 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 the previous summer), or adults (born before the previous summer), by the shape and abrasion of tail feathers (Laaksonen & Lehikoinen 1976).

The tits' foraging locations in pines were studied in relation to ambient temperature (n = 143), amount of snow on the trees (n = 35) and wind speed (n = 69). The observations were divided into the following classes for temperature: (1) mild –1 to +5°C and (2) cold < –5°C; for snow: (1) without snow cover on trees and (2) where a snow layer of more than 5 cm covered most of the outer parts of pines; and for wind: (1) without wind (< 5 km / h) and (2) when the wind speed was > 20 km / h. Data on snow conditions were collected in cold weather, and data on wind conditions were collected in mild weather. To find out whether the tits preferred to forage in the side of the tree exposed to the sun, I recorded whether the majority of individuals of each flock (n = 86) were seen in the sunny or shady side of the tree. Days on which data were collected were chosen so as to avoid intermediate wind speed, intermediate ambient temperatures and intermediate amounts of snow. Thus, the cases included were clearly differentiated.

The size and composition of the flocks studied were determined on the basis of the degree of coherence observed among the birds (Ekman 1979). The hierarchical order of the individuals within each flock was determined by observing the outcome (winners and losers) of agonistic encounters at feeders (Hogstad 1987). The adult male (M) was always the most dominant bird and the juvenile females (f) always the least dominant. The adult female (F) ranked between the juvenile males (m) and the juvenile females. However, because the adult male protects his mate from the juvenile male flock members (Hogstad 1992), the adult female may periodically (when foraging close to her mate) have about the same rank as her mate ($M \approx F > m_1 > m_2 > f_1 > f_2$). I have therefore used age as a

reliable measure of dominance, because dominant males allow their mate to use more protected sites in spite of their lower rank position (Hogstad 1992).

To study the way the birds used pines, individuals were recorded when first observed in the trees. Because predation of tits has been found to vary with their foraging position in trees (Ekman & Askenmo 1984), I recorded whether they were observed within one of the six sectors: trunk, inner half or outer of the branches in the upper or lower halves of pines. I also studied whether their foraging behaviour (foraging or vigilance) was a function of their age when staying in the upper or lower halves of the trees. 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 1988a). 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). The five seconds delay served to eliminate discovery bias since the tits change position rapidly while foraging. To reduce statistical dependence between the observations, only one record was made per individual per tree and no more than five (mostly one or two) records were made of an individual per day. The behaviour of a bird in a tree was unrelated to its behaviour in the previous tree, so I considered the observations to be independent. In total, 247 records were made.

The foraging niche breadth (B) of adults and juveniles in their distribution of positions and substrate use in pines was quantitatively expressed using Levins' index:

$$B = 1 / \Sigma\, p_h^{\,2} \qquad \text{(Eq. 1)}$$

where p_h is the proportion of observations falling in the h^{th} of the six sectors (see Price 1975). The degree of niche overlap between the age groups is quantitatively determined by using of Levins' (1968) equation, in which the overlap index (OI) is:

$$OI = 1 - \tfrac{1}{2}\, \Sigma\, |p_{ah} - p_{jh}| \qquad \text{(Eq. 2)}$$

where p_{ah} and p_{jh} represent the proportion p of adults and juveniles, respectively, in tree sector h.

The time allocated to vigilance and searching for food may also vary with flock size, the bird's social status and ambient temperature. To study the relationship between vigilance behaviour and flock size, I used data on the behaviour of juvenile birds (unaccompanied by adults) observed in the same tree on days with mild weather without a snow cover on the tree surfaces.

Observations were taken between 9.00 a.m. and 14.00 p.m. Frequency data were analysed with two-tailed chi-squared tests using SPSS 20 and significance was accepted at $p \leq 0.05$.

3. Results

3.1. Tree use related to ambient temperature

The pattern of tree use by adult and juvenile Willow Tits varied with temperature (Table 1). As expected, age segregation in foraging height was not fixed, but differed on days with cold weather. In mild weather, without wind or snow on the trees, the juveniles foraged temporarily in subflocks away from the adults, and both adults and juveniles spent about the same amount of time in the upper (adults: 71%, juveniles: 63%) and lower (adults: 29%, juveniles: 37%) halves of pines. At temperatures below –5°C, however, the subflocks reunited into coherent territorial flocks consisting of both adult and juvenile birds, and the juveniles spent significantly less time (17%) in the upper halves of the trees than did the adults (94%; $\chi^2 = 20.20$, df = 1, $p < 0.001$).

There was a non-significant trend towards adult tits using the lower halves more in cold than in mild weather ($\chi^2 = 3.12$, df = 1, $p = 0.08$), while juveniles apparently spent more time in the lower halves in cold weather ($\chi^2 = 12.73$, df = 1, $p < 0.001$; Table 1). Use of the trunk, inner branches and outermost branches by each of the age classes did not differ between mild and cold weather. However, adult and juvenile tits differed in their use of the trunk and inner or outer branches in mild ($\chi^2 = 7.34$, df = 2, $p = 0.025$) and cold weather ($\chi^2 = 9.21$, df = 2, $p = 0.01$). Adults spent most time in

Table 1. Percentage distribution of foraging records of adult and juvenile Willow Tits within the sectors trunk, inner or outer parts of branches in the upper or lower halves of pines in mild weather (ambient temperature –1°C to +5°C) and cold weather (< –5°C) on days in winter with no wind and no snow on the trees.

	Mild weather				Cold weather			
	Adults, *n* = 28		Juveniles, *n* = 81		Adults, *n* = 16		Juveniles, *n* = 18	
	Upper (*n* = 20)	Lower (*n* = 8)	Upper (*n* = 51)	Lower (*n* = 30)	Upper (*n* = 15)	Lower (*n* = 1)	Upper (*n* = 3)	Lower (*n* = 15)
Trunk	10	4	8	1	12	0	5	17
Inner	11	11	33	21	25	0	6	55
Outer	50	14	22	15	56	6	6	11
Mean	71	29	63	37	94	6	17	83

the upper and outermost parts, while juveniles used the lower and innermost parts.

About 60% ($n = 51$) of the tits of 86 flocks were observed in the sunny side of the pines. Although the difference in their use of the sunny vs shady sides was not significant ($\chi^2 = 2.98$, df = 1, $p = 0.08$), there was a trend in preferring the sunny side.

3.2. Tree use related to snowy conditions

On days when snow covered the tree surfaces, adults ($n = 13$) used the upper halves in 39% of the records and the lower halves in 61%, while juveniles ($n = 22$) were observed only in the lower halves ($\chi^2 = 9.87$, df = 1, $p = 0.002$; Table 2).

Adults used the lower and inner parts of the pines significantly more frequently when snow covered the outer tree surfaces than without snow ($\chi^2 = 10.24$, df = 1, $p = 0.001$), while juveniles were only observed in the lower parts and so also differed from the distribution within trees without snow ($\chi^2 = 3.96$, df = 1, $p = 0.046$). Thus, both age classes used the lower part most frequently when the pines were covered with snow.

3.3. Tree use related to windy weather

On days with wind, the Willow Tits avoided the wind exposed side of the pines, and only 4 of 69 observations were from the windy side. I have therefore used data only from the leeward side to compare the groups. Adults (82%) and juveniles (79%) used the lower halves of pines in windy weather (Table 2). Both adults and juveniles moved towards the inner and lower parts of the

Table 2. Percentage distribution of foraging records for adult and juvenile Willow Tits within the sectors trunk, inner or outer parts of branches in the upper or lower halves of pines on days with cold weather in winter without wind, but when the tree surfaces were snow covered, and on days with wind speed more than 20 km / h and when the birds foraged in the leeward sides of pine trees.

	Snow covered tree surface				Windy, leeward side			
	Adults, *n* = 13		Juveniles, *n* = 22		Adults, *n* = 17		Juveniles, *n* = 48	
	Upper (*n* = 5)	Lower (*n* = 8)	Upper (*n* = 0)	Lower (*n* = 22)	Upper (*n* = 3)	Lower (*n* = 14)	Upper (*n* = 10)	Lower (*n* = 38)
Trunk	16	30	0	27	12	29	6	17
Inner	23	31	0	73	6	53	5	48
Outer	0	0	0	0	0	0	10	14
Mean	39	61	0	100	18	82	21	79

Table 3. Niche breadth *B* (Levins' index; can vary from 1 to *n*) of adult and juvenile Willow Tits and their mean niche overlap *OI* (Levins' equation) when foraging in six sectors in winter: trunk, inner half or outer part of the branches in the upper or lower halves in pines under different weather conditions. (Based on Tables 1–2).

Weather	*B* adults	*B* juveniles	*OI* type (niche overlap)
Mild	3.27	4.35	0.67
Cold	2.53	2.82	0.23
Snow	3.77	1.65	0.96
Wind	2.64	3.38	0.81

tree. Thus, although both age groups seek food more frequently towards the trunk and in the lower part of the tree, adults and juveniles differed in their use of the six sectors, mostly due to the more frequent use of the outer parts by juveniles (χ^2 = 5.87, df = 2, p = 0.05).

3.4. Niche breadth and niche overlap between adults and juveniles in their use of pines

The niche breadth of adults in their use of the six sectors in pines was relatively narrow in cold and windy weather, but wider in mild weather and when snow covered the outer parts of the pines (Table 3). The juveniles had the narrowest niche breadths in cold and snowy weather. Except for the adults' broader niche in snowy weather, both age classes narrowed their niche breadth during harsh weather.

The niche overlap between adults and juveniles in their use of the six sectors in pines was low on days with cold weather, but high in mild weather, windy weather and when snow covered the tree surfaces (Table 3). However, the high value for niche overlap in mild weather is misleading because juveniles then foraged in subflocks away from the adults, and thus used the same parts of the pines.

The relatively low overlap value found on cold days was because the adults forced the juveniles into the lower half of the trees. On the other hand, on windy days or when snow covered the pines, the adults foraged more in the inner and lower parts of the trees together with the juveniles, resulting in a relatively high overlap value.

3.5. Vigilance behaviour related to weather and vertical levels in pines

Juvenile Willow Tits were significantly more vigilant than adults under each of the four weather conditions (all χ^2 = 4.86 to 5.66, df = 1, $p < 0.05$). Juveniles were most vigilant in cold weather.

All told, juveniles were significantly more vigilant (0.45) than adults (0.13; χ^2 = 18.80, df = 1, $p <$ 0.001; Table 4). Thus, juveniles spent about three times more of their time on vigilance than adults, and had correspondingly less time for foraging.

The vigilance levels of adults and juveniles did not differ when they used the upper halves of pines in mild, snowy or windy weather (all χ^2 = 2.44 to

Table 4. Mean proportion of time allocated to vigilance by adult (*n* = 75) and juvenile (*n* = 157) Willow Tits when using the upper or lower halves of pines under different weather conditions. Sample size of Upper + Lower is presented in column *n*; Juv:Ad denotes the proportion of vigilance levels of juveniles to adults when combining the upper and lower halves of pines. Upper and Lower are combined when calculating the mean.

	Adults			Juveniles			Juv:Ad
	Upper	Lower	*n*	Upper	Lower	*n*	Up + Low
Mild weather	0.11	0.04	28	0.24	0.14	81	2.6
Cold weather	0.19	0	16	0.17	0.39	18	2.9
Snow on trees	0.08	0	13	0	0.47	19	5.9
Windy	0	0.11	18	0.13	0.28	39	3.7
Mean	0.13			0.45			3.5

3.33, df = 1, n.s.), whereas juveniles were significantly more vigilant than adults in cold weather (χ^2 = 7.20, df = 1, p = 0.007). When seeking food in the lower halves of pines, however, juveniles were significantly more vigilant than adults when snow covered the outer parts of pines (χ^2 = 5.68, df = 1, p = 0.017), but not in mild, cold or windy weather.

The vigilance levels of the birds within each of the age classes did not differ when using the upper or lower halves of pines in the four weather regimes (adults: all χ^2 = 0.03 to 1.73, juveniles: all χ^2 = 0 to 2.88, df = 1, ns).

Table 5. Mean proportion of time allocated to vigilance and foraging by juvenile Willow Tits in different flock sizes when staying in the same tree unaccompanied by dominant adults.

Number of birds	Vigilance	Foraging	*n*
1	0.54	0.46	13
2	0.42	0.58	41
3	0.39	0.61	18
4	0.30	0.70	27
Mean	0.39	0.61	99

3.6. Vigilance behaviour of juveniles related to flock size

There was a negative correlation between the time spent being vigilant and the flock size (Pearson's correlation: r = –0.98, n = 4, p = 0.023; Table 5), and thus a positive correlation with the time spent foraging, which suggests a reduction of costs and an increase of benefits as a consequence of a larger flock size. However, although the vigilance level of a single juvenile (mean = 0.54) was nearly twice that of juveniles in flocks of four (mean = 0.30), the difference was not statistically significant (χ^2 = 2.20, df = 1, p = 0.14).

4. Discussion

Willow Tits apparently select foraging sites that enable them to withstand temporarily adverse weather conditions. Furthermore, they adjust their microhabitat use and vigilance level in response to their perceived risk of predation and starvation. Energetic stress factors such as low ambient temperature, high wind speed, snow cover on the outer tree canopy or hunger, give increased corticosterone (indicator of stress) secretion in small birds (e.g., Scanes *et al*. 1980). Since juvenile Willow Tits in winter flocks have higher plasma levels of corticosterone than adults (Silverin *et al*. 1984), subordinates apparently are more stressed than dominants. Starvation risk increases with decreasing ambient temperatures, and the birds require higher energy reserves to survive the overnight fast (Reinertsen & Haftorn 1983).

The thermal environment, in addition to food availability and predation risk, apparently contributes to foraging choice by small passerines (e.g., Hogstad 1988b). On sunny winter days, small birds like Goldcrests (*Regulus regulus*) (Hogstad 1970) and Willow Tits frequently prefer the tree side exposed to the sun. Furthermore, by shifting from windy sites to the leeward side in pines, they may also save considerably energy in their attempt to balance their energy budgets. Even small changes in wind speeds change the metabolic heat production (Bakken *et al*. 1999). When the wind speed increased from 0.4 to 3.0 m / s, Wolf & Walsberg (1996) estimated that the metabolic rate in small birds increased by 14%. As found earlier by Grubb (1978), I observed that increased wind speed caused a significant decrease in foraging height. Higher wind and lower air temperatures also resulted in more time being spent per tree and less travelling (Grubb 1978).

In the present study, I estimated that adults spent about 85% of their time in pines seeking food, while juveniles spent about 60%. During the few daylight hours, the daily amplitude in body mass in Willow Tits is about 10% expressed as the percentage of morning body mass (Haftorn 1989, Ekman & Lilliendahl 1993). The time needed to reach the critical afternoon body mass to acquire the reserves needed to survive the long night may vary due to interruptions caused by bad weather, predators or competitors. In any case, less foraging time will lower the daily build-up of reserves necessary to meet the nocturnal fasting periods of up to 18–19 hours in mid-winter.

Subordinates experience higher predation rates than dominant adult flock members, apparently because they are frequently forced by the

adults to occupy an area that provides less cover than the area occupied by the dominants (Ekman 1987, Hogstad 1988a, Desrochers 1989, Carrascal & Alonso 2006), thus exposing subdominants to more danger. Hence, in the Budal study area, about 25% and 60% of adults and juveniles, respectively, disappear between December and April each year (Hogstad 1989a). In northern Finland, Koivula *et al*. (1994) found that 17% of the adults and 46% of the juveniles disappeared during the winter, whereas Lahti *et al*. (1997) estimated the winter loss of yearlings to be about 35%. Although males dominate females, there is no marked difference between adult male and female survival rates (Koivula *et al*. 1996, Hogstad unpublished data), probably because the dominant male protects his mate from aggression from other flock members in winter (cf. Hogstad 1992), thus improving the chances of the mate's survival. However, in the Budal study area, the survival rate in winter is higher for juvenile males than juvenile females (Hogstad unpublished data).

Although Willow Tits are organized in a linear dominance hierarchy maintained with little aggression, the aggression observed is positively correlated with temperature (Hogstad 1988b). In mild weather, the tits foraged most frequently in the upper and outer tree canopy where there is most food (cf. Suhonen 1992) and the predation risk is low (Ekman 1986). Since the flocks often split into age-specific subflocks in mild weather, the dominant adults have little influence over the behaviour of subdominants. Then, when given a choice, juveniles selected the more predator protected sites, so the rank-related differences in risk-taking were lacking. In cold weather, however, with increased energy demands and stronger flock coherence, the social dominance hierarchy in the flocks led to the exploitation of unfavourable sites by subordinates. When dominant flock members were temporarily removed, juvenile subordinates increased their use of the more protected sites in the upper halves of the trees (Koivula *et al*. 1994). Therefore, subordination costs are probably one of the main reasons for the higher winter mortality of juveniles, and of juvenile females in particular because of their lowest dominance position.

When the outer canopies of pines were covered by snow, the adults tended to restrict their foraging activities to the inner parts of the lower halves of the trees, i.e. the same sectors as the juveniles most frequently visited. Then, as the niche breadth of adults decreased and niche overlap between adults and juveniles increased, the juveniles were forced to increase their vigilance, resulting in less time to seek food.

Small owls and Sparrowhawks prey more on the lower outer than the inner parts of conifers (Ekman 1986), a microhabitat frequently used by Willow Tits. Some differences in the foraging niches of high- and low-ranked Willow Tits are therefore probably related to differences in predation vulnerability and the importance of seeking cover. Adults got the most secure sites and juveniles the least secure ones. Therefore, not unexpectedly, more subordinates than dominants tend to be killed by small owls (Ekman 1986, Suhonen *et al*. 1993).

Apart from causing mortality, predators can induce food shortage due to repeated attacks that discourage the tits from feeding places and disturb them so often that their flight costs are increased and the time they have for feeding and foraging is reduced. The tits therefore spend more time on vigilance before they start to feed again after an attack. A field experiment showed that juvenile Willow Tits returned to a feeder before dominant adults after life-like predator models mounted close to the feeder were removed, revealing that subordinates took the greatest predator risks (Hogstad 1988c), probably because of different hunger levels. The birds therefore had to adjust their time and microhabitat use as a response to their perceived risk of starvation and predation. When extra food was provided, the number of Willow Tits killed by small owls decreased (Jansson *et al*. 1981), and low-ranked flock members improved their winter survival significantly (Hogstad 1988d).

The present study shows that juvenile Willow Tits in flocks of four members that stayed in the same tree spent 12% or 24% more time searching for food than birds in flocks of two or solitary birds, respectively, indicating that individuals in larger flocks may have a higher rate of food intake than in smaller ones, and thus increased benefits as a consequence of larger flock size. Beauchamp (1998) found that the addition of three to four individuals appeared to be needed to double the mean food intake rate of a solitary bird. Willow Tits in

flocks of three members were found to have higher plasma levels of corticosterone than in flocks containing four or five birds (Silverin *et al*. 1984). Obviously, the time spent watching for predators influences the birds negatively. If the time an individual has to allocate to vigilance is inversely dependent on its energy demand, the advantages of flocking should increase with the demand for food. Because the risk of being predated decreases with the flock size, birds should participate in flocks when energy demands are high. Thus, flocks that have split into subgroups of adults and juveniles reunite immediately after an alarm signal is given (Ekman 1987). This suggestion is strengthened by field experiments performed in winter: Willow Tits that had access to supplemented food flocked less (Ekman 1987, Hogstad 1988d), and Great Tits (*Parus major*) and Blue Tits (*Cyanistes caeruleus*) flocked more often, both in periods without access to supplemented food and in cold and windy conditions (Berner & Grubb 1985). Reduced energetic stress obviously plays an important role in determining differences in behaviour related to flock coherence.

Because flocks of juveniles may also split into subflocks of two members when the temperature rises, there must be some disadvantages associated with living in large flocks. As birds are relatively more aggressive on days with relatively high temperatures (e.g., Caraco 1979, Hogstad 1988a, c) than on cold days, aggression may be suppressed on cold days due to energetic stress. However, although formation of winter flocks allows Willow Tits to maintain higher collective vigilance and survival, formation of large flocks was restricted by low-ranked juvenile males (Hogstad 1989b).

To sum up, Willow Tits selected microhabitats to withstand harsh weather and minimize the risk of starvation and predation. Socially dominant adults selected foraging sites to minimize predation risk, whereas subordinate juveniles were forced by adults to forage in more predator risky places. It may therefore be suggested that, although a high level of vigilance by juveniles reduces the short-term predation risk, it may lead to a long-term decrease in fitness because high vigilance may induce food shortages and thus be the main cause of the higher winter mortality of juveniles compared to that of adults.

However, even though juveniles lose time for seeking food when close to dominant adults, adult company is not only a disadvantage. Juveniles capitalize on the greater experience of the adults, and adults are important in alerting flock members to the presence of predators (Alatalo & Helle 1990, Hogstad 1995) and thus influence the winter survival rate of the juveniles. Furthermore, flock membership may be their only chance to breed in the area the following spring (Hogstad 2003).

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Vädrets inverkan på födosök och vaksamhet hos övervintrande talltitor beror på individens sociala status

Födosök och vaksamhet hos talltitan (*Poecile montanus*) studerades under olika väderförhållanden i en subalpin tallskog i mellersta Norge under vintrarna 2009–2013. Fåglarna ändrade både vistelseplats i träden och grad av vaksamhet i förhållande till predationsrisk och behov av föda. Vid låga temperaturer födosökte de dominanta vuxna fåglarna huvudsakligen i de övre och mest predationssäkra delarna av träden, medan de subdominanta unga fåglarna rörde sig i lägre partier av trädet där predationsrisken var högre. När grenarna var täckta av snö, tenderade vuxna fåglar att söka föda i de innersta och lägre delarna av trädet och överlappade då tydligt med de unga.

I blåsiga förhållanden höll sig ungfåglar längre ut på grenarna än de vuxna. Ungfåglar var också klart mer vaksamma och använde ca 60 % av tiden till födosök, medan de vuxna använde runt 85 %. Vi föreslår att den höga vaksamhetsnivån hos de subdominanta ungfåglarna är energetiskt kostsam och kan vara huvudorsaken till att de har en högre vinterdödlighet än de vuxna.

References

Alatalo, R.V. & Helle, P. 1990: Alarm calling by individual Willow Tits *Parus montanus*. — Animal Behaviour 40: 437–442.

Bakken, G.S., Reynolds, P.S., Kenow, K.P., Korschgen, C.E. & Boysen, A.F. 1999: Metabolic response to air temperature and wind in day-old mallards and a stan-

dard operative temperature scale. — Physiological and Biochemical Zoology 72: 656–665.

Beauchamp, G. 1998: The effect of group size on mean food intake rate in birds. — Biological Reviews of the Cambridge Philosophical Society 73: 449–472.

Berner, T.O. & Grubb, T.C., Jr. 1985: An experimental analysis of mixed-species flocking in birds of deciduous woodland. — Ecology 66: 1229–1236.

Bradley, J.V. 1968: Distribution-free Statistical Tests. — Prentice Hall, London.

Brotons, L. 1997: Changes in the foraging behaviour of the Coal Tit (*Parus ater*) due to snow cover. — Ardea 85: 249–257.

Caraco, T. 1979: Time budgeting and group size: a test of theory. — Ecology 60: 618–827.

Carrascal, L.M. & Alonso, C.L. 2006: Habitat use under latent predation risk. A case study with wintering forest birds. — Oikos 112: 51–62.

Cooper, S.J. 2000: Seasonal energetics of Mountain Chickadees and Juniper Titmice. — Condor 102: 635–644.

Desrochers, A. 1989: Sex, dominance and microhabitat use in wintering Black-capped Chickadees: a field experiment. — Ecology 70: 636–645.

Ekman, J. 1979: Coherence, composition and territories of winter social groups of 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 53: 119–134.

Ekman, J. 1986: Tree use and predator vulnerability of wintering passerines. — Ornis Scandinavica 17: 261–267.

Ekman, J. 1987: Exposure and time use in Willow Tit flocks: the cost 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. & Lilliendahl, K. 1993: Using priority to food access: fattening strategies in dominance-structured Willow Tit (*Parus montanus*) flocks. — Behavioral Ecology. 4: 232–238.

Grubb, T.C. 1978: Weather-dependent foraging rates of wintering woodland birds. — Auk 95: 370–376.

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. 1989: Seasonal and diurnal body weight variations in titmice, based on analyses of individual birds. — Wilson Bulletin 101: 217–235.

Hogstad, O. 1970: Movements of winter flocks of Goldcrests, *Regulus regulus* (L.). — Nytt Magasin for Zoologi 18: 33–39.

Hogstad, O. 1987: Social rank in winter flocks of Willow Tits *Parus montanus*. — Ibis 129: 1–9.

Hogstad, O. 1988a: Rank-related resource access in winter flocks of Willow Tit *Parus montanus*. — Ornis Scandinavica 19: 169–174.

Hogstad, O. 1988b: Advantages of social foraging of Willow Tits *Parus montanus*. — Ibis 130: 275–283.

Hogstad, O. 1988c: Social rank and antipredator behaviour of Willow Tits *Parus montanus* in winter flocks. — Ibis 130: 45–56.

Hogstad, O. 1988d: The influence of energy stress on social organization and behaviour of Willow Tits *Parus montanus*. — Fauna Norvegica Ser. C, Cinclus 11: 89–94.

Hogstad, O. 1989a: Subordination in mixed-age bird flocks – a removal study. — Ibis 131: 128–134.

Hogstad, O. 1989b: 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. 1992: Mate protection in alpha pairs of wintering Willow Tits, *Parus montanus*. — Animal Behaviour 43: 323–328.

Hogstad, O. 1995: Alarm calling by Willow Tits, *Parus montanus*, as mate investment. — Animal Behaviour 49: 221–225.

Hogstad, O. 2003: Strained energy budget of winter floaters in the Willow Tit as indicated by ptilochronology. — Ibis 145: E19–E23.

Jansson, C., Ekman, J. & von Brömssen, A: 1981. Winter mortality and food supply in tits, *Parus* spp. — Oikos 37: 313–322.

Koivula, K., Lahti, K., Rytkönen, S. & Orell, M. 1994: Do subordinates expose themselves to predation? Field experiments on feeding site selection by Willow Tits. — Journal of Avian Biology 25: 178–183.

Koivula, K., Orell, M. & Rytkönen, S. 1996: Winter survival and breeding success of dominant and subordinate Willow Tits *Parus montanus*. — Ibis 138: 624–629.

Laaksonen, M. & Lehikoinen, E. 1976: Age determinations of Willow and Crested Tit *Parus montanus* and *P. cristatus*. — Ornis Fennica 53: 9–14.

Lahti, K., Koivula, K. & Orell, M. 1997: Dominance, daily activity and winter survival in Willow Tits: detrimental cost of long working hours? — Behaviour 134: 921–939.

Lendrem, D.W. 1983: Predation risk and vigilance in the Blue Tit (*Parus caeruleus*). — Behavioral Ecology and Sociobiology 14: 9–13.

Levins, R. 1968: Evolution in changing environments. — Princeton Univ. Press, Princeton, N.J.

Price, P.W. 1975: Insect Ecology. — New York: John Wiley & Sons.

Reinertsen, R.E. & Haftorn, S. 1983: Nocturnal hypothermia and metabolism in the Willow Tit *Parus montanus* at 63°N. — Journal of Comparative Physiology 151B: 109–118.

Scanes, C., Merill, G.F., Ford, R., Mauser, P. & Horowitz,

C. 1980: Effects of stress (hypoglycaemia, endotoxin, and ether) on the peripheral circulating concentration of corticosterone in the domestic fowl (*Gallus domesticus*). — Comparative Biochemistry and Physiology C 66: 183–186.

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.

Suhonen, J. 1992: Predation risk influences the use of foraging sites by tits. — Ecology 74: 1197–1203.

Suhonen, J., Halonen, M. & Mappes, T. 1993: Predation risk and the organization of the *Parus* guild. — Oikos 66: 94–100.

Villen-Perez, S., Carrascal, L.M. & Seoane, J. 2013: Foraging patch selection in winter: a balance between predation risk and thermoregulation benefit. — PLOS ONE 8: DOI: 10.1371

Wachob, D.G. 1996: The effect of thermal microclimate on foraging site selection by wintering Mountain Chickadees. — Condor 98: 114–122.

Wolf, B.O. & Walsberg G.E. 1996: Thermal effects of radiation and wind on a small bird and implications for microsite selection. — Ecology 77: 2228–2236.