Social rank and winter survival in the Willow Tit *Parus montanus*

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The dominance hierarchy and the effect of the social status on survival was studied in 18 winter flocks of the Willow Tit near Oulu northern Finland in 1986–87. The flocks were small and stable groups that usually consisted of an adult pair and a pair of yearlings, which were never descendants of their older group companions. In general, males were ranked higher than the females. Within sex groups, adults dominated yearlings. The birds with long tarsi dominated individuals with shorter ones. Wing length was not correlated with social status. The size variables had no effect on rank order in group members of the same age and sex.

The dominant individuals had higher survival rate than the subordinates. In juvenile birds the survival rate of high-ranking individuals was higher in both sexes. Reasons for these differences, and explanations for the existence of subordination as a strategy, are discussed. Subordinates, although having a higher mortality rate, are supposed to have even higher one if they adopt a solitary way of life. Several benefits attached to living in groups evidently outweigh the costs caused by dominant individuals.

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Introduction

Dominance hierarchies are a widespread phenomenon in bird flocks. The linear model first described by Schjelderub-Ebbe (1922) in the Domestic Hen *Gallus gallus* is commonly reported for a variety of bird species. In the linear rank order there is only one individual in every hierarchical stage. In North American and European Paridae this kind of hierarchy has been described for several species (e.g. Dixon 1965, Glase 1973, Smith 1976, Hegner 1985, Hogstad 1987).

Willow Tits *Parus montanus* live in small coherent flocks between the breeding seasons (e.g. Ekman 1979). Ekman & Askenmo (1984) and Hogstad (1987) have reported somewhat differing results from their studies of dominance ranks in these groups. According to Ekman & Askenmo (1984), adult birds always dominate over yearlings, while Hogstad (1987) reported that the relationships between the age groups are more complicated.

In addition to descriptive studies, little information exists on the population ecological consequences of the hierarchies. Most papers deal with the relationships between rank and reproductive success in mammal societies (see Dewsbury 1982 for a review). Asymmetry in access to resources — namely dominants excluding the subordinates from the food sources, forcing them to go to poorer feeding sites or to less safe habitats — has been documentated in some bird species (Krebs et al. 1972, Glase 1973, Baker et al. 1981, Ekman & Askenmo 1984, Schneider 1984, Hegner 1985, de Laet 1985). Direct field evidence that these asymmetries would have real fitness consequences, for example on mortality, are rare (but see Fretwell 1969, Kikkawa 1980, Ekman & Askenmo 1984).

Here we present results of a one year field study on wintering Willow Tits. The aim of this work was to investigate how age, sex and body size affect the social status and whether rank is associated with winter survival.

Material and methods

The data were collected between October 1986 and November 1987 near Oulu in northern Finland. The study area covers about 11 km^2 of mainly Norwegian spruce *Picea abies* and Scots pine *Pinus sylvestris* forests of different ages, from open clear-cuttings and bogs to closed forests (for details see Orell & Ojanen 1983). The winter population was relatively dense in 1986/87 — about 170 birds in 40 flocks.

The rank order in 13 flocks was measured in winter 1986/87 and that of 5 flocks in autumn 1987. The birds were captured using mist-nets at the feeders, several of which (2–4 per flock) were established inside the winter territory of each group. At the feeders a cut of fat hung on a wire from a tree branch. No food was provided after the birds were captured and the dominance relationships were determined. When captured, the birds were marked individually with coloured plastic rings. Their wing lengths were measured to the nearest millimetre using the maximum chord method (Svensson 1984). Tarsus lengths were measured using a sliding caliper, with an accuracy of 0.05 mm. Age determination was based on tail feather characteristics (Laaksonen & Lehikoinen 1976). The birds which had wing and tarsus lengths (own unpubl. data) near the observed minimum (≤ 62 mm and ≤ 16 mm) and maximum (≥ 65 mm and ≥ 17 mm) lengths of the population studied were sexed as females and males, respectively (see also Haftorn 1982). The majority of the birds were, however, sexed according to the incubation patch and differences in parental behaviour when their nests were searched in summer 1987. In the Oulu area Willow Tits start breeding in early May (Orell & Ojanen 1983). The birds that were observed after 1 May were considered survivors and those that disappeared were counted as being dead.

The ranking of the birds in the hierarchies was based on several interactions observed between two birds at the feeders. Only the flocks in which each two bird combination was tested were included in the data. Three criteria were used in estimating social dominance. The bird was dominant if it (1) chased the other bird away from the feeder, (2) caused the withdrawal of another individual from the feeder, or (3) was feeding and made the other bird to wait for its turn (see also Hogstad 1987). Criteria 2 and 3 were used with caution to avoid incorrect interpretations caused by withdrawals and waitings that were not real. The similarity of rankings made by both authors independently of each other confirmed the validity of these criteria. There were only very few contradictory outcomes in two-bird interactions. If a bird was a winner once, it was nearly always superior in future conflicts, too. The rank order was therefore easily determined.

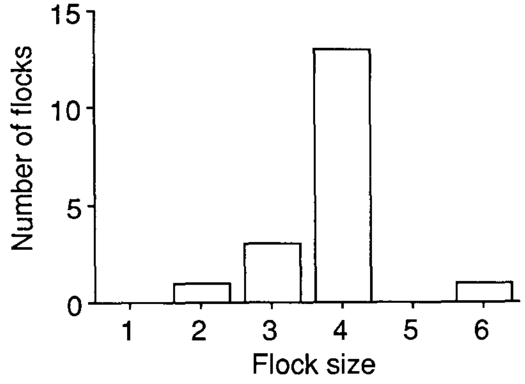

Fig. 1. Frequency distribution of the flock sizes. Floater individuals (see text) not included.

In most cases the "flock" was a clear unit. Individuals changing their group were rare. Two birds in our data were considered as winter floaters, they switched regularly from flock to another during the winter (see Ekman 1979, Smith 1984).

Results

The most common group size was that of four birds (Fig. 1). In the most typical flock there was a pair of old birds having bred together in the previous summer, and a pair of yearlings. However, the yearlings were never the offspring of the old pair. The flocks were extremely closed groups which roamed within a restricted area, defined as "group territory" by Ekman (1979).

Old males were the highest in the hierarchy, with one exception, and those lowest in the hierarchy were nearly always young females. In general, males dominated females (1-tailed binomial test: $P<0.001$, Table 1). The males were superior to females in both age groups (in adults $P=0.012$, in yearlings $P= 0.014$, Table 1). Old birds tended to be higher in the hierarchy than yearlings (Table 1). To remove the effect of sex the effect of age was studied within the sex groups. In males, the adults clearly dominated the yearlings (1-tailed binomial test: $P<0.001$ Table 1).

Table 1. Rank relations in different age and sex classes. The frequencies indicate occasions when a member of a particular group was above or below another individual in the hierarchy.

	Above in hierarchy			
	Adult male	Juvenile male	Adult female	Juvenile female
Below in hierarchy				
Adult male	–	1	1	0
Juvenile male	16	11	8	7
Adult female	10	6	–	0
Juvenile female	7	21	4	6

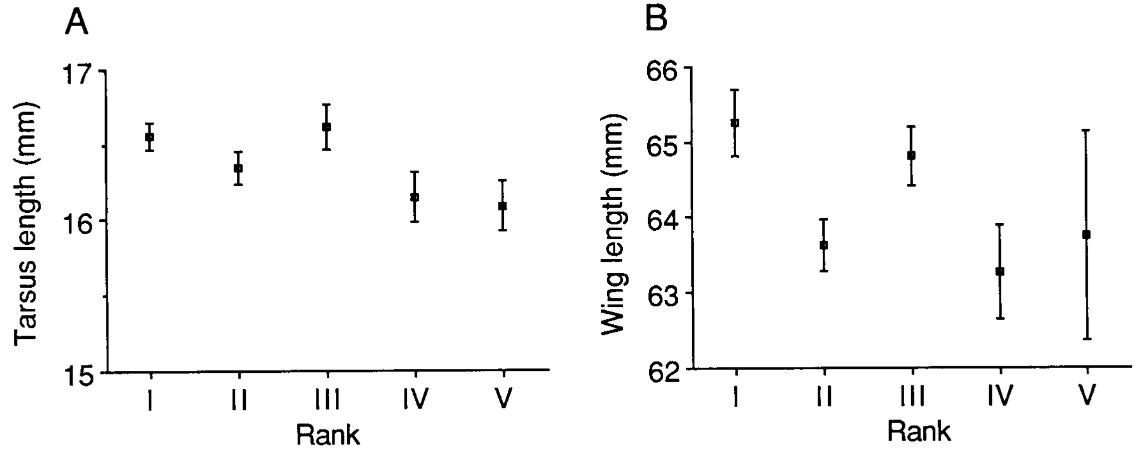

Fig. 2. Relationship (Spearman correlation) between social rank and (A) tarsus length, and (B) wing length. Means with SD. The correlation is fairly significant in (A) ($r_s = -0.27$, $P<0.05$, $n=61$), but not in (B) ($r_s = -0.21$, $P<0.1$, $n=63$).

Also in females adult individuals were always (four cases) above their younger group companions, but the number of observations was low and the relation remained nonsignificant. The length of the tarsus is the most reliable measure for determining body size (Garnett 1976). There was a significant negative correlation between the length of the tarsus and the social status (Fig. 2A). The body size seemed to affect social rank, although the correlation between the wing length and social status was nonsignificant (Fig. 2B). However, it must be noted that the sexual size dimorphism may bias the results. Males that were highest in the hierarchy also had the longest tarsi and wings. Therefore, we made pairwise comparisions, where the sizes of group companions belonging to the same age and sex class were compared. In these 17 dyads (Table 1) the winners were as follows :

Winner	
Longer wing	10
Shorter wing	4
Longer tarsus	11
Shorter tarsus	6

Larger individuals seemed to be superior over smaller ones, but the tendencies were not significant (1-tailed sign test: wing length P=0.090, tarsus length P= 0.166). Stationary individuals were superior to intruders; both floater individuals were ranked in the

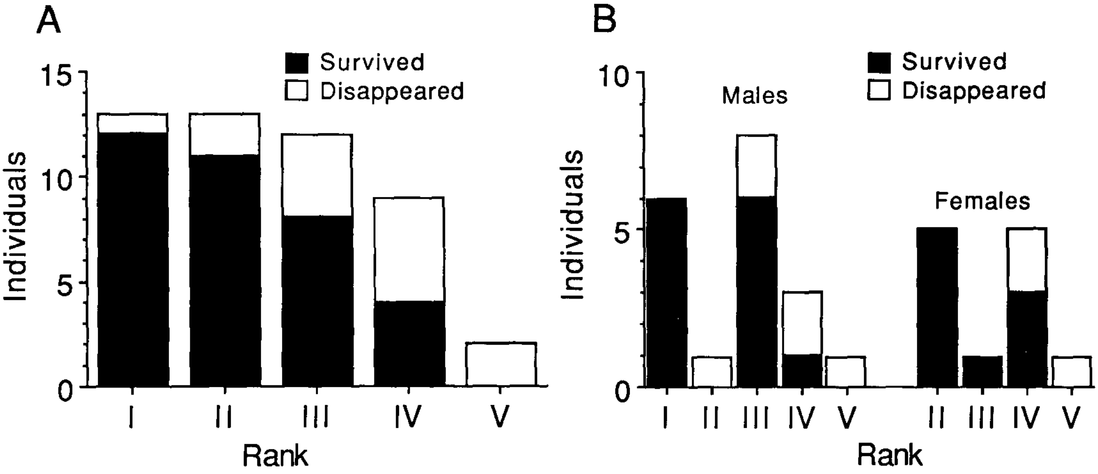

Fig. 3. Relationship between the social status and survival from mid-winter to the beginning of the breeding season. (A) All age groups included and (B) sex groups in yearlings separately. The survivors had significantly higher ranks than the nonsurvivors, 1-tailed Mann-Whitney U-tests: (A) z=3.17, P< 0.001 and (B) males: U=16, P=0.025, females: U=3, P=0.025.

bottom category (5) in every flock which they were regular members.

A total of 35 (71%) of the 49 birds studied in winter 1987 survived from the beginning of February to the breeding season. There was a clear relationship between rank and survival. High-ranking birds did significantly better than the low-ranking ones (Fig. 3A). When the age groups were separated it showed that in yearlings, but not in adults, the ranks of survivors were significantly higher than than those of nonsurvivors (1-tailed Mann-Whitney U-tests, for yearlings U=44.5, P=0.002, for adults U=13, P> 0.05). In yearlings, both the females and the males that survived had significantly higher ranks than the nonsurvivors (Fig. 3B). Those birds which were no longer observed and were assumed dead could, of course, have emigrated outside the study area in the spring. However, there was no significant correlation between social rank and the distance from the feeder the bird most often used to the later nesting site (males: r_s=–0.278, ns, n=19, females: r_s=0.162, ns, n=15), as could be expected if the lower survival rate of subordinates was an artefact due to their longer dispersal distances in the spring.

Discussion

The winter flocks studied were similar to Willow Tit groups reported by Ekman (1979) from southern Sweden. In both areas the most common flock size was four. It differed from the typical group size of six found in central Norway (Hogstad 1987). Hogstad's view was that the larger group size in his study area could be due to the absence of group companions belonging to other tit species. European tits form large mixed-species flocks in areas where several species coexist. In single-species flocks the number of representatives of a particular species should be larger than in mixed-species flocks to achieve equal benefits attached to group life, for example improved feeding efficiency and protection against predation (e.g. Pulliam & Millikan 1982). In our study area only occasionally did a pair of Crested Tits *Parus cristatus* join the flocks. In most cases, the flocks were groups comprising four Willow Tits only. Therefore, our results do not support Hogstad's idea.

In Paridae the superiority of males has been documentated also in other species (e.g. Kluyver 1957, Smith 1976, Järvi & Bakken 1984, Hegner 1985). Relationships between adult females and young males were not as clear as could be concluded from Ekman & Askenmo (1984), who reported that the adults were nearly always above juveniles (111 cases out of 119). Our results suggest a more complex alternative. In six cases the young male was above the adult female. In eight cases the opposite was true (Table 1). Within the sex groups a young male was above an adult male only once. Adult females were always above juvenile females. These findings agree with Hogstad (1987). It must be noted that the study of Ekman & Askenmo (1984) was made in natural conditions, where the interactions between adult females and young males could have been rarer than in our feeders. The superiority of adults in their data could therefore be an artefact produced by the conditions existing where the observations were made.

The positive relationship between size and social rank has been reported earlier in the Willow Tit, as well as in some other tit species (Garnett 1976, Smith 1976, Järvi & Bakken 1984, Hegner 1985, Hogstad 1987). However, the present data does not allow distinction properly between the effects of sex, age and body size on rank. Our limited data within sex and age groups cannot provide evidence of larger individuals being superior.

Improved survival rate in the high-ranking individuals was particular clear in juvenile birds. The same phenomenon has been noted in some other species (Fretwell 1969, Smith 1976, Kikkawa 1981) and also in Willow Tits (Ekman & Askenmo 1984). In the data of Ekman & Askenmo the high-ranking birds were also nearly always the oldest individuals. Therefore, they could not separate the effects of age and rank on survival. The higher survival rate of the high-ranking birds could, of course, have been caused by other age-bound factors than the social status (e.g. general experience). Our results indicate that rank can lead to differences in survival also within the age and sex groups. Further, these differences do not result from the possible rank-dependent differences in dispersal distances.

Among captive Great Tits *Parus major*, the dominant individuals were able to displace subordinates from the food sources they had found (Krebs et al. 1972). In studies of Baker et al. (1981) the food intake of low-ranking Dark-eyed Juncos *Junco hyemalis* was reduced because the dominants displaced them from food patches. Differences in food intake may not be large enough to cause differences in mortality. Millikan et al. (1985) found in mixed junco flocks that the food intake of Grey-headed Juncos *Junco caniceps* was improved at the expense of subordinate Dark-eyed Juncos but, despite this, individuals belonging to both species got enough food for their daily needs.

Ekman et al. (1981) showed that rings of subordinate Willow Tits were more often found in prey remnants of the Pygmy Owl *Glaucidium passerinum* than those of dominant individuals. According to Ekman & Askenmo (1984), dominant individuals exclude the subordinates from upper parts of the trees. These parts are evidently safer feeding sites as can be concluded from the little time allocated to predator surveillance there (Ekman 1987). Other authors have also showed that when feeding, the subordinates are forced to take greater risks in the presence of predators (de Laet 1985, Hegner 1985) or are displaced to less safe feeding sites (Schneider 1984). Because we have no field evidence to present here we cannot say whether it was predation or starvation that caused the differences in mortality.

The short-term fitness loss of the subordinates was clear. Therefore, it is not probable that in the Willow Tit dominance and subordination could be two different alternatives of a mixed strategy, where the behavioural morphs would be maintained in a population by frequency-dependent selection. According to this idea, the dominants would suffer extra costs — for example frequent fights (Rohwer & Ewald 1981, Møller 1987) — due their social status. These costs would outweigh the benefits of being dominant, thereby equalizing the short-term fitness in the dominance classes (Rohwer & Ewald 1981). Then why do the subordinates join dominant individuals? Why do they not leave the group and adopt a solitary way of life, without the pressure caused by the dominants? Winter territories of the flocks are large (in our study area about 27 ha), surely allowing separate living.

One explanation is that the young subordinates take the risks of subordination to gain the possibility of replacing the dominant individuals later when they die. The adults dominated the juveniles within the sex groups. The juveniles, therefore, have a possibility to take the place of an adult of their own sex in the future and they could possibly be considered "hopeful dominants" that are waiting for a vacancy for a despot to open (West-Eberhard 1975).

It seems clear that the solitary way of living is a worse alternative, even taking into account costs that could be avoided outside the group. Floaters, individuals which are not regular members of any group, suffer from very high mortality (Ekman et al. 1981). However, the factors that prevent floaters from gaining membership may also cause the higher mortality among them and not the solitariness *per se*. On the other hand, Ekman (1987) noted that even the subordinates of larger groups gain more advantages in terms of reduced time allocated to vigilance compared with individuals living in pairs. This saves time which thereby can be used for other activities important to survival, for example feeding and food storing. This, and presumably other yet unknown benefits, can explain why the subordinates are so "sheepish".

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Selostus: **Sosiaalinen asema ja hengissä säilyvyys talvisissa hömötiaisparvissa**

Hömötiaisen talviparvien sosiaalista hierarkiaa ja sen vaikutusta yksilön säilyvyyteen tutkittiin Oulussa syksystä 1986 syksyyn 1987. Yksilöiden väliset sosiaaliset suhteet määritettiin 18 parvesta lintujen talvireviireille perustetuilla ruokintapaikoilla. Hierarkkisen aseman määrityksessä käytettiin kolmea kriteeriä. Yksilö tulkittiin toiseen nähden dominantiksi, mikäli se (1) syrjäytti tämän ruokintapaikalta suoraan ajamalla, (2) aiheuttamalla lähestymisellään toisen poistumisen tai (3) pakottamalla alisteisen linnun odottamaan ruokintapaikan läheisyydessä vuoroaan.

Parvet olivat pieniä käsittäen 2–6 lintua. Tavallisin parvikoko oli neljä. Useimmiten parvessa oli alueella pesinyt vanha pariskunta ja niiden seuraan lyöttäytyneinä 2–4 nuorta lintua. Nämä eivät koskaan olleet vanhan pariskunnan jälkeläisiä. Tutkimusalueen tiaisparvet olivat lähes puhtaita hömötiaisryhmiä, joten muiden lajien läsnäolo ei selitä parvikoon pienuutta.

Hierarkiassa koiraat olivat keskimäärin naaraita ylempänä. Vanhat koiraat olivat yhtä poikkeusta lukuun ottamatta ylimpänä parvissaan. Hierarkian alin lintu oli useimmiten nuori naaras. Vanhat linnut dominoivat samaa sukupuolta olevia nuorempia yksilöitä. Kokomuuttujista nilkan pituus oli yhteydessä sosiaaliseen asemaan: pitkänilkkaiset olivat ylimpänä. Siiven pituus ei selittänyt asemaa hierarkiassa. Samanikäisten ja samaa sukupuolta olevien parvikumppaneiden väliseen arvojärjestykseen yksilön koolla ei ollut merkitsevää vaikutusta. Vanhat yksilöt eivät tämän työn perusteella kaikissa tapauksissa ole nuoria ylempänä toisin kuin aikaisemmin on esitetty.

Hierarkiassa ylimpänä olleet linnut säilyivät helmikuun alusta pesimäkauteen selvästi paremmin kuin alisteiset. Säilyvyyserot eivät johtuneet alisteisten taipumuksesta siirtyä pesimään dominantteja etäämmäksi talvireviiriltään. Myöskään muut mahdolliset ikään tai sukupuoleen sidotut tekijät eivät aiheuttaneet säilyvyyseroja; nuorillakin linnuilla, jotka olivat samaa sukupuolta, asema hierarkiassa oli yhteydessä säilyvyyteen. Vaikka alisteiset kärsivätkin jäsenyydestään parvessa, ryhmäelämään liittyy ilmeisesti etuja, joista luopuminen olisi vieläkin heikompi vaihtoehto kuin dominanttien sietäminen.

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