

Rank-dependent fattening strategies of Willow Tit *Parus montanus* and Crested Tit *P. cristatus* mixed flock members

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I studied changes in body mass in response to the presence of heterospecifics in mixed-species flocks of free-living Willow and Crested Tits. Body reserves of Willow Tits as subordinate flock members were found to be dependent on the presence of dominant Crested Tits. At dusk, Willow Tits were heavier than Crested Tits. Body reserves of members of mixed-species flocks negatively correlated with dominance rank within both intraspecific and interspecific hierarchies. Removal experiments confirmed results of field observations, revealing a causal relationship between rank and ability to choose the safest fattening strategy. Body mass and fat reserves of Willow Tit alpha males decreased in the absence of Crested Tits. In contrast, body mass and fatness of dominant individuals of Crested Tits remained at the same level. To control for changes in body mass resulting from a higher rank and smaller flocks, the foraging height of remaining individuals of both species was recorded. Willow Tits responded to removal of Crested Tits by foraging closer to the top of the tree. No shifts were observed in groups with only Crested Tits. Fattening strategies dependent on social status represent a flocking cost to individuals belonging to a subordinate species. Further investigations should be done into the benefits of mixed-species flocking, which is a social behaviour common in parids.



1. Introduction

Temperate zone parids often spend the non-breeding season as members of mixed-species flocks. The field observations (Alerstam et al. 1974, Alatalo et al. 1986) and experiments (Alatalo et al. 1985, 1987) have shown that interspecific competition restricts access to food (Hogstad 1988a) and the safest and most preferred feeding sites (Ekman 1979, Hogstad 1988b, Krams 1996). Only dominant individuals in dominance-structured groups have prior access to the contested resources and this may show up in the form of better winter survival (Ekman et al. 1981, Koivula & Orell

1988, Koivula et al. 1996). In contrast to the survival advantages of dominants, subordinates usually pay for their membership in both single- and mixed-species groups by higher mortality rates (Ekman 1986, Hogstad 1988b, 1989).

Thus, functionally, even when a dominant's food supply can be considered predictable, a subordinate's will remain unpredictable. Consequently, it was found that in a single-species flock, subordinates respond to these unpredictable conditions by acquiring and carrying extra body reserves (roughly equivalent to fat reserves) as a buffer against periods of high energy demand or food shortage when dominants are most likely to

take advantage of their higher rank (Ekman & Hake 1990, Ekman & Lilliendahl 1993, Clark & Ekman 1995). Although more body reserves reduce the risk of starvation (Lehikoinen 1986, Ekman & Hake 1990), extra body mass also imposes a survival cost by increasing the risk of predation (Blem 1975, Lima 1986, McNamara & Houston 1990, Witter et al. 1994).

Mixed-species flocking appears to be a common form of parid social organization (Morse 1970, Hogstad 1978, Ekman 1979). Heterospecifics in these flocks are generally considered to substitute for conspecifics as protection against predators at a lower competition cost (Alatalo et al. 1986). However, when comparing the advantages of conspecific versus heterospecific groups, existing data show little evidence that heterospecific groups are an advantage (Hogstad 1988a). More data are, therefore, needed on the costs and benefits of the two social groups.

This paper deals with fattening strategies of members of mixed-species flocks composed of Willow Tits *Parus montanus* and Crested Tits *P. cristatus*. The possible dependence of the fattening strategies of the Willow Tit, as a subordinate species, on the presence of the Crested Tit individuals might indicate a flocking cost to the subordinates.

2. Material and methods

2.1. Study area and species

I studied body reserves in an individually colour-marked population of free-living Willow Tits and Crested Tits in an approximately 60-year-old forest of Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*. Because of the many small semi-open bogs and areas of saplings, the forests are highly fragmented.

Data were collected between January and the middle of February 1994 and in October 1995 near the town of Krāslava (55°47'N, 27°12'E), in southeastern Latvia. The first study winter was mild with little snow on the ground and trees. There were some cold spells below -15°C in the beginning of October 1995.

All members of ten mixed-species flocks containing equal numbers of Crested Tits (mean

number of individuals = 4.0) and Willow Tits (mean number of individuals = 4.0) had been sexed and aged (as adult or juvenile) either in the previous breeding season or during the study period. The shape of the rectrices of Willow and Crested Tits (Laaksonen & Lehikoinen 1976) and the colour of the iris of Crested Tits (Lens & Dhondt 1992) were used to determine age. The sexual dimorphism in wing and tarsus length was used for sexing individuals (Koivula & Orell 1988).

2.2. Dominance hierarchies

Dominance order was measured within each flock by observing pairwise interactions between birds at temporary feeders filled with sunflower seeds and fat. During observations at feeders, I recorded between 79 and 98 aggressive encounters per flock (total 850). To determine individual rank, I followed the procedures of Koivula and Orell (1988). The intraspecific dominance-subordinate relationships were linear and stable in all the flocks. In the interspecies hierarchy only one exception was recorded where a Willow Tit alpha male was above a Crested Tit subordinate female. However, a lack of other reversals in the dominance hierarchy confirmed previous reports (Hogstad 1978, Ekman 1979, Ekman & Askenmo 1984, Krams 1996) that Crested Tits dominate Willow Tits, males dominate females and, within sexes, adults generally dominate juveniles.

2.3. Body mass

When examining the feeding efficiency of dominant and subordinate individuals of each species, I used repeated weighings on different days of all members of a flock. The weight of birds was measured on an electronic balance (BLTK-500), with a precision of 0.1 g. I collected data on weight at the last hour of the birds' daily activity period and took only one measurement per bird a day. In total, 429 weighings of Crested Tits and 360 weighings of Willow Tits were recorded with 11 as the mean number of measurements per individual for Crested Tits and 8 per individual for Willow Tits.

Differences between the dominant and subordinate species in the way evening body mass varied among individuals was tested by using relative body mass. The evening body mass was transformed into the body mass index (BMI) by taking the ratio of body mass to wing-length³, to scale body reserves according to size (Summers 1988). Extra fat may be costly because it decreases maneuverability and results in a slower take-off. Since the cost is manifested through wing-loading, wing length should be of biological significance for fat reserves (McNamara & Houston 1990, Witter et al. 1994). To avoid possible changes in individual wing lengths, this parameter was measured 5–7 times per study period, and I used medians of individual birds for calculating the BMI.

2.4. Removal experiments

I removed all of the Crested Tits in five groups to test whether the correlation between rank in a mixed-species flock and body reserves represents a causal relationship. The remaining Willow Tits in the experimental flocks, which were allowed to rise in rank to become the dominant species, were compared with Crested Tits in flocks where all of the Willow Tits were removed to control body reserves for changed flock size and seasonal effects.

Flock size is important to wintering birds as protection against predators (Elgar 1989, McNamara & Houston 1992, Lima 1995). The risk of attack by predators may increase as the size of a flock is reduced. In theory, body reserves of individuals should decrease under conditions of higher predation risk (McNamara & Houston 1990). To distinguish between the higher risk of predation as the size of a flock is reduced and the increased opportunity for foraging as an individual's rank in the flock rises, I observed the same individuals before and after removal from a flock and their changes in selection of foraging sites. Birds foraging near the tops of trees are better protected against attacking predators (Ekman 1986, Krams 1996). To control for changes in body mass resulting from a higher rank and smaller flocks, I observed the height of foraging of the dominant individuals of both species which were not taken

away from their territories during the study. Foraging height was transformed into relative height with 0 as ground level and 1 as the top of trees.

Tits removed from the flocks were caught in the morning as early as possible, immediately brought to indoor cages and provided with *ad libitum* sunflower seeds and dried arthropods. The remaining individuals were then observed for a week. Longer removal periods were not possible because neighbouring Willow Tits began to immigrate into the experimental plots (Desrochers 1988).

2.5. Risk of predation

In the study area, the Sparrowhawk *Accipiter nisus* is the principal diurnal predator of the wintering tits (Krams 1996). On average, I observed the predators every day. Tits and Great-spotted Woodpeckers *Dendrocopos major* were the most frequently preyed-upon birds at my study site. Although the tit flocks often used to split up into temporal subflocks, Sparrowhawks were observed to appear at any time of the day and, probably because of this, the flocks of wintering tits were highly coherent.

3. Results

3.1. Individual body reserves

No significant differences in body mass of Willow Tits (one-way ANOVA, $F_{39} = 3.89$, $p > 0.05$) and Crested Tits ($F_{39} = 2.72$, $p > 0.05$) were apparent from the period between 1994 and 1995; therefore, I pooled the data obtained for each species for further analysis.

No significant heterogeneity was found in the body mass of Willow Tits of different ranks (one-way ANOVA, $F_{3,40} = 11.33$, $p > 0.05$, Table 1) whereas variations in body mass between individual Crested Tits were significant ($F_{3,40} = 23.35$, $p < 0.05$, Table 2). Comparisons between ranks showed that Crested Tit alpha individuals were the heaviest flock members (Tukey-type post hoc, $p < 0.05$).

In comparisons of body reserves carried by the birds during the last hour of activity, signifi-

cant differences in the BMI were found both among Willow Tits (Kruskal Wallis one-way ANOVA, $H = 87.41$, $n = 40$, $p < 0.01$, Table 1) and Crested Tits ($H = 59.11$, $n = 40$, $p < 0.01$, Table 2). Although in theory only the most dominant birds have unrestricted access to food, the Willow Tit males (alpha and beta individuals) carried significantly less body reserves towards the end of their daily activities than their mates did (Tukey-type post hoc, $p < 0.05$). A similar pattern was also observed in the Crested Tit where females were significantly fatter than their mates (Tukey-type, $p < 0.05$).

This pattern of greater body reserves in subordinate flock members became even more evident in comparisons of the BMI between tit species where the BMI gradually became higher as rank decreased from dominant Crested Tit alpha males to the most subordinate Willow Tit females (2-tailed Spearman rank correlation coefficient $r_s = 0.89$, $p = 0.012$, Tables 1 and 2). One exception was noted, Willow Tit adult males carried less body reserves than Crested Tit subordinates (2-tailed Mann-Whitney test, $U = 11$, $n_1 = 10$, $n_2 = 10$, $p < 0.05$, Tables 1 and 2). Furthermore, being subordinate birds in the interspecific hierarchy, Willow Tits did not only have more body reserves but they also had more stable body mass in the evening which is shown by comparisons of the

body mass coefficient of variation (2-tailed Mann-Whitney test, $U = 63$, $n_1 = 40$, $n_2 = 40$, $p < 0.01$, Tables 1 and 2).

3.2. Removal experiment

The removal experiments confirmed a causal link between rank and the amount of body reserves. Body mass and the BMI of all five experimental dominant individuals of the Willow Tit became smaller in response to removal of dominant Crested Tits (Fig. 1). The response was consistent among all Willow Tits studied (1-tailed binomial test, direction predicted, $p < 0.05$); their average BMI decreased from $41.33 \pm 0.53 \text{ kg/m}^3$ to $39.73 \pm 0.47 \text{ kg/m}^3$ (mean of individual medians of BMI and SE) during the removal period. Mean body mass of individuals decreased about $0.55 \pm 0.04 \text{ g}$ ($\pm \text{SE}$). In contrast, the BMI of dominant Crested Tit individuals remained almost at the same level (Fig. 1). A change of only $0.03 \pm 0.01 \text{ g}$ ($\pm \text{SE}$) was recorded in the mean individual body mass of experimental Crested Tits.

As soon as dominant Crested Tits were removed from the groups, Willow Tits responded by foraging closer to the tops of trees (Fig. 2). Before the removal experiment, Willow Tit alpha males foraged mainly in the central parts of the

Table 1. Body reserves of Willow Tits by sex and rank (means of medians for individual birds, SE). N = number of individuals.

	Males		Females	
	Dominant	Subordinate	Dominant	Subordinate
Body mass (g)	11.5 ± 0.05	11.76 ± 0.08	11.3 ± 0.04	11.01 ± 0.039
BMI (kg/m^3)	41.1 ± 0.52	43.4 ± 0.47	43.3 ± 0.45	45.8 ± 0.48
CV of body mass	1.71 ± 0.37	1.11 ± 0.23	1.44 ± 0.23	1.23 ± 0.17
N	10	11	9	10

Table 2. Body reserves of Crested Tits by sex and rank (means of medians for individual birds, SE). N = number of individuals.

	Males		Females	
	Dominant	Subordinate	Dominant	Subordinate
Body mass (g)	12.5 ± 0.07	12.8 ± 0.09	12.2 ± 1.0	12.13 ± 0.097
BMI (kg/m^3)	37.5 ± 0.53	40.3 ± 0.52	40.2 ± 0.49	42.8 ± 0.51
CV of body mass	1.68 ± 0.22	1.08 ± 0.15	1.2 ± 0.17	0.98 ± 0.10
N	10	11	10	9

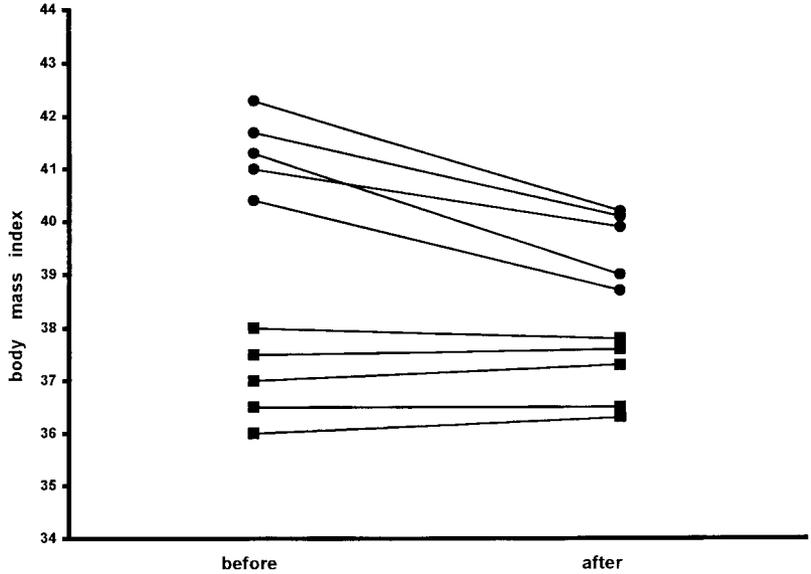


Fig. 1. The effect on the body mass index of Willow Tits (N = 5, circles) from rising in rank after removal of Crested Tits, and Crested Tits (N = 5, squares) after removal of Willow Tits.

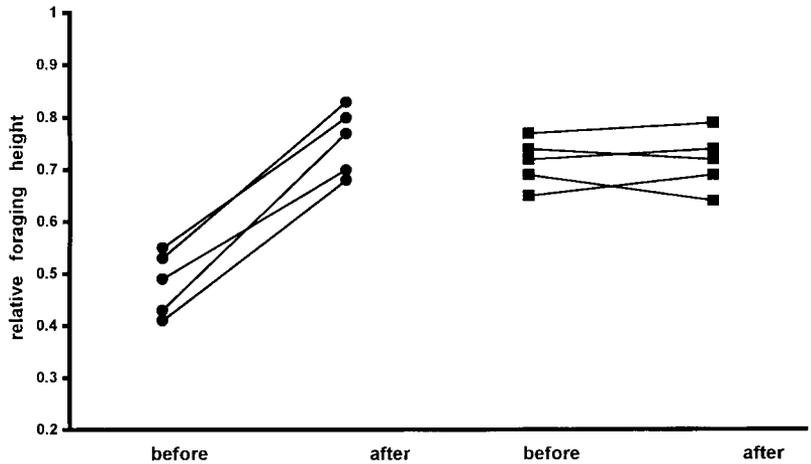


Fig. 2. The effect on relative foraging height of Willow Tits (N = 5, circles) from rising in rank after removal of dominant Crested Tits, and Crested Tits (N = 5, squares) with Willow Tits excluded.

pine canopy (0.48 ± 0.23 , mean of individual medians of relative foraging height and SE). After the removal of Crested Tits, all five experimental Willow Tits noticeably changed their foraging height (1-tailed binomial test, direction predicted, $p < 0.05$) to the upper parts of the canopy (0.76 ± 0.32 , mean of individual median of relative foraging height and SE, Fig. 2). No similar shifts were observed in groups with only Crested Tits (Fig. 2). In this way, Willow Tits supposedly lowered the probability of being attacked by avian predators.

4. Discussion

Within either species there were no significant differences in body mass between old and young males and between old and young females where social conflicts are probably more pronounced. This confirms the idea that body size and mass alone can not determine dominance rank in social groups formed by conspecifics (Wilson 1975).

In contrast, in comparisons of body reserves where individual size was controlled for through the BMI, Willow Tits, as a subordinate species,

carried more body reserves. There is some previous empirical evidence that subordinate individuals increase body mass and accumulate fat reserves during their daily activities (Ekman & Lilliendahl 1993). In my study area, Willow Tits and the most subordinate Crested Tits had greater body reserves despite foraging difficulties at their feeding stations, which as a rule are more exposed to predators (Ekman 1987, Suhonen 1993a, b, Krams 1996), and thus, the birds require more time for vigilance (Ekman 1987). The energetic costs in a subordinate's time budget probably might be compensated for by a greater abundance of arthropods in the outer parts of trees such as spruce (Suhonen et al. 1992). However, the extra body reserves that correspond to more unpredictable access to food resources suggests that body reserves are under control of a foraging strategy and are not simply related to food availability (McNamara & Houston 1990). This fattening strategy of subordinate Willow Tits no doubt lowers the probability of energetic shortfalls. Extra reserves in subordinate flock members could be a buffer against times of limited food resources, for example, when dominants claim their right of access to food (Ekman & Lilliendahl 1993, Clark & Ekman 1995). This is likely mainly during cold spells or severe winters. Not surprisingly, I found no starvation in Willow Tits as variations in winter temperatures were not very severe during my study. It is also known that limited food resources can constrain fattening strategies in subordinate individuals of dominance-structured flocks, thereby, resulting in less body reserves (Koivula et al. 1995). This was not the case in my study; all Willow Tit individuals carried greater body reserves than dominant Crested Tits. Moreover, the evening body mass of Willow Tits was less variable than that of Crested Tits. The observed relative variability of body mass and smaller fat reserves of Crested Tits could be explained by foraging predictability rather than the result of a dominance cost (Hogstad 1987) or starvation (Jansson et al. 1981). Otherwise, dominants with their lower body reserves would be at a higher risk of energetic shortfall than subordinates. These facts apparently suggest that both tit species individuals foraged optimally maintaining a neutral energy balance regardless of rank.

It was also found that strategic control of reserves can produce the opposite pattern where

dominant Willow Tits carried the highest energy reserves even when food resources can not be limited (Hogstad 1987). With their analytical model, Verhulst and Hogstad (1996) showed that the optimal level of energy resources is highest in dominant individuals when social dominance affects predation risk, but not food supply. My conflicting results may be explained by the unpredictable risk of predation in the fragmented habitats. Although in my study area social dominance clearly affected the risk of predation (Krams 1996), frequent changes of habitats may increase the risk especially on the habitat edges, and dominants could temporarily lose their right to ensure their safety. Thus, under such conditions a bird with smaller body reserves may have a better chance of evading a predator.

In general, relative body mass gradually increased as rank decreased from top-ranking Crested Tits to subordinate Willow Tits. Despite an observed overlap in the BMI between adult Willow Tit males and juvenile Crested Tit females, the results obtained suggest the influence of individuals of the dominant species on the fattening strategies of their congeneric flock-mates. The results of the removal experiments also confirmed the suggestion that deposition of energy reserves in Willow Tits was dependent on the presence of Crested Tits. Thus, Willow Tits could be considered to be substitutes for the missing low-ranking individuals of the dominant species (Alerstam et al. 1974, Buskirk 1976, Hogstad 1988a), since replacement of their metabolized energy was dependent on the influence of Crested Tits. However, the relative body mass of dominant Willow Tit individuals never reached the Crested Tit level. It could be explained by the effect of neighbouring Crested Tits visiting the territories of experimental flocks after removal of resident Crested Tits.

If individuals belonging to a dominant species monopolize high-quality resources (Hogstad 1988c, Koivula et al. 1994) and even the fattening strategies of their flock-mates of a subordinate species suggest a flocking cost, why do two or more tits of different species join in the mixed-species groups? While in a mixed-species flock, individual foragers may devote more time to feeding as the size of the group increases without any increase in their personal risk of being preyed upon

(Hogstad 1988a). Besides collective detection, foragers enjoy the benefits of their personal vigilance (Lima 1994, Krams 1998). The use of time as a currency for trading costs and benefits here is based on the assumption that the use of time is important to fitness. Although in winter the social hierarchy of free-roaming tits is reported to be maintained with little aggression (Ekman & Askenmo 1984, Hogstad 1987), in mixed-species flocks the interference levels could be even lower, allowing social individuals to devote more time to foraging and vigilance, which may outweigh the above flocking costs of individuals belonging to a subordinate species.

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Selostus: Hömö- ja työttötiäisen päivittäinen painonvaihtelu riippuu yksilön asemasta talviparvessa

Kirjoittaja tutki hömö- ja työttötiäisen päivittäistä painonkehitystä lajien muodostamissa talvisissa sekaparvissa Latviassa. Parven sisäinen hierarkia vaikutti päivän aikana kerätyn ravintorasvan määrään siten, että parven alisteisilla jäsenillä oli illalla suhteellisesti suuremmat rasvavarastot. Rasvan määrää arvioitiin painoindeksillä. Hömötiäisillä alisteisena lajina oli keskimäärin enemmän varastorasvaa kuin työttötiäisellä, ja samoin lajien sisäisessä hierakiassa alemmalla tasolla olevat yksilöt olivat pulskempia kuin hierarkiassa korkealla olevat yksilöt (Taulukot 1 ja 2). Kirjoittaja tutki myös kokeellisesti vaikuttiko asema parvessa yksilön painonkehitykseen. Viidestä koeparvesta hän poisti työttötiäiset ja vertasi näiden parvien hömötiäisyksilöiden painonkehitystä kontrolliparvissa havaittuun painonkehitykseen. Kontrolliparvista oli poistettu kaikki hömötiäiset. Kaikissa koeparvissa hömötiäisten painoindeksi aleni työttötiäisten poiston seurauksena, mutta kontrolliparvien työttötiäisten painoindeksit eivät muuttuneet

(Kuva 1). Tulos tuki havaintoaineiston johtopäätöstä, että päivittäinen painonkehitys riippuu yksilön asemasta parvessa. Koeparven hömötiäiset lisäksi muuttivat ruokailupaikkojaan suhteellisesti korkeammalle puussa sen jälkeen kun työttötiäiset oli parvesta poistettu. Kontrolliparvien työttötiäiset eivät muuttaneet ruokailupaikkojaan hömötiäisten poiston seurauksena (Kuva 2). Tämä tulos osoittaa, että lajien välinen kilpailu rajoittaa hömötiäisten ruokailupaikkojen valintaa, kun taas työttötiäiset ovat sekaparvissa aina kykeneviä ruokailemaan paremmilla ruokailupaikoilla puiden latvuksissa. Kirjoittaja pohtii optimaalisia tapoja kerätä rasvavarastoja suhteessa hierakiseen asemaan. Alisteisten yksilöiden taipumus kerätä enemmän ihonalaista rasvaa toimii luultavasti puskurina ravinnon väliaikaista puutetta vastaan. Huonoissa ravintotilanteissa hierarkiassa korkeimmalla olevilla yksilöillä on ensisijainen pääsy ravintokohteisiin. Dominanttien yksilöiden ei näin ollen tarvitse kantaa suuria rasvavarastoja mukanaan, varsinkin kun on mahdollista, että suuret ihonalaiset rasvavarastot tekevät lintuyksilön alttiimmaaksi pedoille.

References

- Alatalo, R. V., Gustafsson, L., Linden, M. & Lundberg, A. 1985: Interspecific competition and niche shifts in tits and the goldcrest: an experiment. — *J. Anim. Ecol.* 54: 977–984.
- Alatalo, R. V., Gustafsson, L. & Lundberg, A. 1986: Interspecific competition and niche changes in tits (*Parus spp.*): evaluation of nonexperimental data. — *Am. Nat.* 127: 819–834.
- Alatalo, R. V., Eriksson, D., Gustafsson, L. & Larsson, K. 1987: Exploitation competition influences the use of foraging sites by tits: experimental evidence. — *Ecology* 68: 284–290.
- Alerstam, T., Nilsson, S. G. & Ulfstrand, S. 1974: Niche differentiation during winter in woodland birds in southern Sweden and the island of Gotland. — *Oikos* 25: 321–330.
- Blem, C. R. 1975: Geographic variation in wing-loading of the House Sparrow. — *Wilson Bull.* 87: 543–549.
- Buskirk, W. H. 1976: Social systems in a tropical forest avifauna. — *Am. Nat.* 110: 293–310.
- Clark, C. W. & Ekman, J. 1995: Dominant and subordinate fattening strategies: a dynamic game. — *Oikos* 72: 205–212.
- 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 the willow tit *Parus montanus* and the crested tit *P. cristatus*. — *Ornis Scand.* 10: 56–68.
- Ekman, J. 1986: Tree use and predator vulnerability of wintering passerines. — *Ornis Scand.* 17: 261–267.
- Ekman, J. 1987: Exposure and time use in willow tit flocks: the cost of subordination. — *Anim. Behav.* 35: 445–452.
- Ekman, J. & Askenmo, C. E. H. 1984: Social rank and habitat use in willow tit groups. — *Anim. Behav.* 32: 508–514.
- Ekman, J., Cederholm, G. & Askenmo, C. 1981: Spacing and survival in winter groups of willow tit *Parus montanus* and crested tit *P. cristatus* – a removal study. — *J. Anim. Ecol.* 50: 1–9.
- Ekman, J. B. & Hake, M. K. 1990: Monitoring starvation risk: adjustments of body reserves in greenfinches (*Carduelis chloris* L.). — *Behav. Ecol.* 1: 62–67.
- Ekman, J. B. & Lilliendahl, K. 1993: Using priority to food access: fattening strategies in dominance-structured willow tit (*Parus montanus*) flocks. — *Behav. Ecol.* 4: 232–238.
- Elgar, M. A. 1989: Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. — *Biol. Rev.* 64: 13–33.
- Hogstad, O. 1978: Differentiation of foraging niche among tits, *Parus* spp., in Norway during winter. — *Ibis* 120: 139–146.
- Hogstad, O. 1987: Social rank in winter flocks of willow tits *Parus montanus*. — *Ibis* 129: 1–9.
- Hogstad, O. 1988a: Advantages of social foraging of willow tits *Parus montanus*. — *Ibis* 130: 275–283.
- Hogstad, O. 1988b: Rank-related resource access in winter flocks of willow tits *Parus montanus*. — *Ornis Scand.* 19: 169–174.
- Hogstad, O. 1988c: Social rank and antipredator behaviour of willow tits *Parus montanus* in winter flocks. — *Ibis* 130: 45–56.
- Hogstad, O. 1989: Subordination in mixed-age bird flocks – a removal study. — *Ibis* 131: 128–134.
- Jansson, C., Ekman, J. & von 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.
- Koivula, K., Lahti, K., Rytönen, S. & Orell, M. 1994: Do subordinates expose themselves to predation? Field experiment on feeding site selection by Willow Tits. — *J. Avian Biol.* 25: 178–183.
- Koivula, K., Orell, M., Rytönen, S. & Lahti, K. 1995: Fatness, sex and dominance: seasonal and daily body mass changes in Willow Tits. — *J. Avian Biol.* 26: 209–216.
- Koivula, K., Orell, M. & Rytönen, S. 1996: Winter survival and breeding success of dominant and subordinate Willow Tits *Parus montanus*. — *Ibis* 138: 624–629.
- Krams, I. A. 1996: Predation risk and shifts of foraging sites in mixed willow and crested tit flocks. — *J. Avian Biol.* 27: 153–156.
- Krams, I. 1998: Dominance-specific vigilance in the Great Tit. — *J. Avian Biol.* 29. (In press.)
- Laaksonen, M. & Lehikoinen, E. 1976: Age determination of willow and crested tit *Parus montanus* and *P. cristatus*. — *Ornis Fennica* 53: 9–14.
- Lehikoinen, E. 1987: Seasonality of the daily weight cycle in wintering passerines and its consequences. — *Ornis Scand.* 18: 216–226.
- Lens, L. & Dhondt, A. A. 1992: Variation in coherence of crested tit winter flocks: an example of multivariate optimization. — *Acta Oecol.* 13: 553–567.
- Lima, S. L. 1986: Predation risk and unpredictable feeding conditions: determinants in body mass in birds. — *Ecology* 67: 377–385.
- Lima, S. L. 1994: On the personal benefits of anti-predatory vigilance. — *Anim. Behav.* 48: 734–736.
- Lima, S. L. 1995: Back to the basics of anti-predatory vigilance: the group-size effect. — *Anim. Behav.* 49: 11–20.
- McNamara, J. M. & Houston, A. I. 1990: The value of fat reserves and the tradeoff between starvation and predation. — *Acta Biotheor.* 38: 37–61.
- McNamara, J. M. & Houston, A. I. 1992: Evolutionary stable levels of vigilance as a function of group size. — *Anim. Behav.* 32: 986–993.
- Morse, D. H. 1970: Ecological aspects of some mixed species foraging flocks of birds. — *Ecol. Monogr.* 40: 119–168.
- Suhonen, J. 1993a: Predation risk influences the use of foraging sites by tits. — *Ecology* 74: 1197–1203.
- Suhonen, J. 1993b: Risk of predation and foraging sites of individuals in mixed-species tit flocks. — *Anim. Behav.* 45: 1193–1198.
- Suhonen, J., Alatalo, R. V., Carlson, A. & Höglund, J. 1992: Food resource distribution and the organization of the *Parus* guild in a spruce forest. — *Ornis Scand.* 23: 467–474.
- Summers, R. W. 1988: The use of linear measurements when comparing masses. — *Bird Study* 36: 77–79.
- Verhulst, S. & Hogstad, O. 1996: Social dominance and energy reserves in flocks of Willow Tits. — *J. Avian Biol.* 27: 203–208.
- Wilson, E. O. 1975: *Sociobiology*. — Belknap Press, Harvard Univ. Press, Cambridge, Massachusetts.
- Witter, M. S., Cuthill, I. S. & Bonser, R. H. C. 1994: Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. — *Anim. Behav.* 48: 201–222.