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INDIVIDUALS ADJUST THEIR BODY RESERVES TO
DOMINANCE POSITION WITHIN MIXED FLOCKS
OF THE WILLOW (*PARUS MONTANUS*) AND THE CRESTED
TIT (*P. CRISTATUS*): A FIELD EXPERIMENT

ABSTRACT: Mixed-species flocks represent a prevalent sociality form of the forest wintering parids. Efficient use of time is of high survival value for individual foragers. It was found that in groups composed of willow (*Parus montanus*) and crested tits (*P. cristatus*) intraspecific competition appears to be more severe than interspecific interference. Decreasing time allocated to intraspecific aggressiveness, social individuals in mixed-species flocks supposedly increase their probability of survival till the next breeding season. Social dependence of the two tit species was controlled by observations of their fattening strategies. Willow tits were considered to substitute for the lacking crested tits, since replacement of their metabolized energy was found to be dependent on the influence of dominant crested tits.

KEY-WORDS: mixed-species flocks, willow tits, crested tits, body reserves, aggressive interactions, benefits and costs.

1. INTRODUCTION

By forming groups, small insectivorous birds of the *Paridae* guild may reduce their risk of being preyed upon (Ekman et al. 1981) because of improved vigilance in single-species or multi-species flocks (Hogstad 1988b). However, the flocking costs and benefits among the flock members are not equal due to the competition (Alatalo et al. 1986). Within tit groups dominance hier-

archies are established in which heavier-bodied species dominate others (Hinde 1952). Within each single species in turn, males generally dominate females and adults dominate juveniles. Dominants have better access to crucial resources such as cover against predators and food (Smith 1976, Hogstad 1987). The dominant individuals usually defend the resources against subordinate conspeci-

fics and heterospecifics (Hogstad 1988c). This results in better winter survival of high-ranked flock members at least in the willow tit (*Parus montanus*) (Ekman and Askenmo 1984, Koivula and Orell 1988) and the black-capped chickadee (*P. atricapillus*) (Smith 1984). Predation and energy stress are considered as main factors responsible for winter mortality of parids (Ekman et al. 1981, Ekman 1986).

Fat reserves in winter resident bird species are adaptively adjusted to increased requirements through winter fattening (Newton 1969, Lehtikoinen 1987). Since food availability varies with both long-term variations and short-term fluctuations, and metabolic requirements vary over time, the higher level of fat reserves may increase a probability of winter survival. However, many birds appear to maintain fat reserves at levels lower than what they could achieve (King 1972), indicating that fattening strategies are under adaptive control. Although larger reserves reduce the risk of starvation, they also impose a survival cost by increasing risk of predation (Witter et al. 1994).

Due to the interference competition, subordinates may be faced with more unpredictable foraging conditions than dominants since finding food in winter could be less predictable than any other season. Recent observations (Ekman and Lilliendahl 1993, Gosler et al. 1995) reveal that this additional foraging uncertainty under the risk of predation is countered by a more intensive hedging strategy. That is, subordinates in the flocks of the great tit (*P. major*) and the willow tit maintain larger body reserves than dominants, suggesting the impact of intraspecific competitive interactions.

The mixed-species flocking appears to be a prevalent form of parid social organi-

zation (Morse 1970, Hogstad 1978, Ekman 1979). However, the existing data actually trying to quantify the influence of conspecific and heterospecific company for the value of sociality do not show clear advantage of heterospecific company (Hogstad 1988a). Heterospecifics in the mixed-species flocks are generally considered to substitute for conspecifics as predator protection at low competition cost (Alatalo et al. 1986). However, the net benefit of improved predator protection at decreased intraspecific competition may be reduced by rising costs of interspecific competition.

I studied duration and intensity of competition among mixed-species flock members composed of dominant crested tit (*P. cristatus*) and subordinate willow tit using common food resources. The study was carried out in a productive coniferous habitat where sparrowhawks (*Accipiter nisus*) were present. Since the individuals involved in an agnostic encounter generally are not considered to be vigilant, predation risk supposedly should rise with increasing intensity of competition. Further, body reserves of subordinate parids in mixed-species flocks may be influenced by the presence of dominant congeneric individuals. In this case one can expect interspecific interference to be of lower intensity than intraspecific competitive interactions. This may lower the intensity of aggressive interactions among a mixed-species flock's members decreasing the risk of predation that in turn can suggest an advantage of heterospecific flocking. Otherwise, if interspecific interference increases, other factors such as habitat complexity and predator skill should contribute much more to variations in composition and group size as an anti-predator device.

2. MATERIAL AND METHODS

2.1. STUDY PLACE AND THE BIRDS

I studied agnostic interactions and body reserves in an individually colour-marked population of free-living willow tits and crested tits in middle-aged forest of Scots pine (*Pinus sylvestris*). The data was collected between January and the beginning of March 1995 near the town Krāslava (55°47' N, 27°11' E), south-eastern Latvia. The study winter was mild with little snow on the ground and trees. The average temperature of the coldest month (January) was -3°C and only one cold spell occurred with temperatures down to -15°C .

All members of ten mixed-species flocks containing crested tits (mean number of individuals = 3.1, SE = 0.54) and willow tits (mean number of individuals = 4.9, SE = 0.78) 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 and Lehtikoinen 1976) and the colour of the iris of crested tits (Lens and Dhondt 1992) were used to determine age. The sexual dimorphism in wing and tarsus length was used for sexing (Koivula and Orell 1988).

2.2. DOMINANCE HIERARCHIES

Dominance order was measured within each flock using pairwise interactions between birds at temporary feeders provided with sunflower seeds and fat. During observations at feeders I recorded between 73 and 88 aggressive encounters per flock (total 770). To determine individual rank I followed the procedures of Koivula and Orell (1988). Within each dyad, the individual was considered to be dominant if it won significantly more interactions than the other (sign-test, 2-tailed). The dominance-subordi-

nate relationships were linear and stable in all the flocks. Absence of permanent reversals in the dominance hierarchy confirmed previous reports (Hogstad 1978, Ekman 1979, Ekman and Askemo 1984, Krams 1996) that crested tits dominate willow tits, males dominate females and, within sex, adults generally dominate juveniles. There was only one exception in the interspecific hierarchy where an alpha male of the willow tit was above a subordinate female of the crested tit.

2.3. AGGRESSIVE BEHAVIOUR

To measure timing and frequency of parid interference, I divided their encounters into three categories: (1) supplanting attacks, in which the dominant individual flies at and takes over the place of a more subordinate bird; (2) chases; and (3) fights, when two fighting individuals come into physical contact. All aggres-

sive encounters ($n = 204$) were recorded by a stop-watch when the birds foraged both at and away from the feeders. The duration and frequency of agnostic interactions among seven mixed-species flocks were studied after the procedures of dominance measurements.

2.4. BODY WEIGHT

When examining feeding efficiency of dominant and subordinate individuals of each species, I used repeated weighings on different days of individuals of the ten flocks. The birds were caught and their weight was recorded on an electronic balance (BLTK-500), with a precision of 0.1 g. Only one recording was taken per bird in a day. I collected weight data at the last hour of the birds' daily activity period. A set of 341 weighings of crested tits and 343 weighings of willow tits was obtained with 11 as the mean number of measurements per individual for crested tits and 7 per individual for willow tits. To ensure sufficient replication I used medians of each individual bird ($n = 80$) as the independent observa-

tion for statistical testing and I used two-tailed Mann-Whitney U-test with the Bonferroni correction of significance levels.

In order to test differences between the dominant and subordinate species in the way evening body mass varied among individuals, relative body mass was used: the evening body mass was transformed into a body mass index by taking the ratio of body mass to $(\text{wing-length})^3$, to scale body reserves by size. Carrying fat may be costly due to decreased manoeuvrability and slower take-off. Since the cost operates through wing-loading, wing-length should be of biological significance for the fat reserves (Ekman and Lillendahl 1993, Witter et al. 1994).

3. RESULTS

3.1. INTENSITY OF AGGRESSIVE ENCOUNTERS

In general, the overall level of aggression among flock-members seemed to be rather low. During a total of 130 hr of observation, aggressive encounters were recorded with a mean value of 1.6 per hr per flock. Males were more aggressive than females among willow tits and crested tits and initiated 88% and 92% of all attacks, respectively, despite the nearly even sex ratio.

The three categories of intraspecific interference of both tit species differed in their duration (Table 1). Physical combats were the most durable aggressive encounters and they were observed the least (4.4% of all encounters). It should be noted that all of the fights were observed close to the artificial feeding sites. Both willow and crested tits chased conspecifics occasionally (10.8%). The mean duration of a chase was significantly shorter

Table 1. Duration (s) of intraspecific and interspecific aggressive interactions of willow and crested tits

	Intraspecific		Inter-specific
	Willow tits	Crested tits	
Supplanting attacks	0.25	0.24	0.23
SE	0.009	0.008	0.008
n	61	68	44
Chasing	3.12	3.04	—
SE	1.223	0.954	
n	10	12	
Fight	3.59	3.67	—
SE	0.302	0.282	
n	4	5	

than the duration of a fight (t-test, $p > 0.05$, Table 1). Supplanting attacks were the shortest in duration (Table 1) but most frequent intraspecific interactions (84.8%). There were significant differences in the duration of fights (t-test, $p > 0.05$), chases (t-test, $p > 0.05$) and supplanting attacks (t-test, $p > 0.05$) between the two species. Interspecific encounters were observed at lower rates

than intraspecific aggression of both the tit species (21.6%), and they may be considered as milder aggressive interactions due to the lack of real fights and even chases (Table 1). The duration of interspecific supplanting attacks did not differ from the mean duration of intraspecific supplanting attacks of the species (t-test, $p > 0.05$).

3.2. INDIVIDUAL BODY RESERVES

Subordinate willow tits carried larger body reserves towards the end of the daily activity than did dominants. The pattern of larger reserves of subordinates became evident in comparisons of fatness of all mixed-species flock members where individual size was controlled for through the body mass index. This index which gradually increased from dominant crested tits to subordinate willow tits (Fig. 1, Tables 2, 3). There was no difference in body mass index only between juvenile females of the crested tit and adult males of the willow tit (2-tailed Mann-Whitney U-test, $U = 7$, $n_1 = 9$, $n_2 = 3$, $p > 0.05$). Subordinate willow tits had not merely larger body reserves but they had

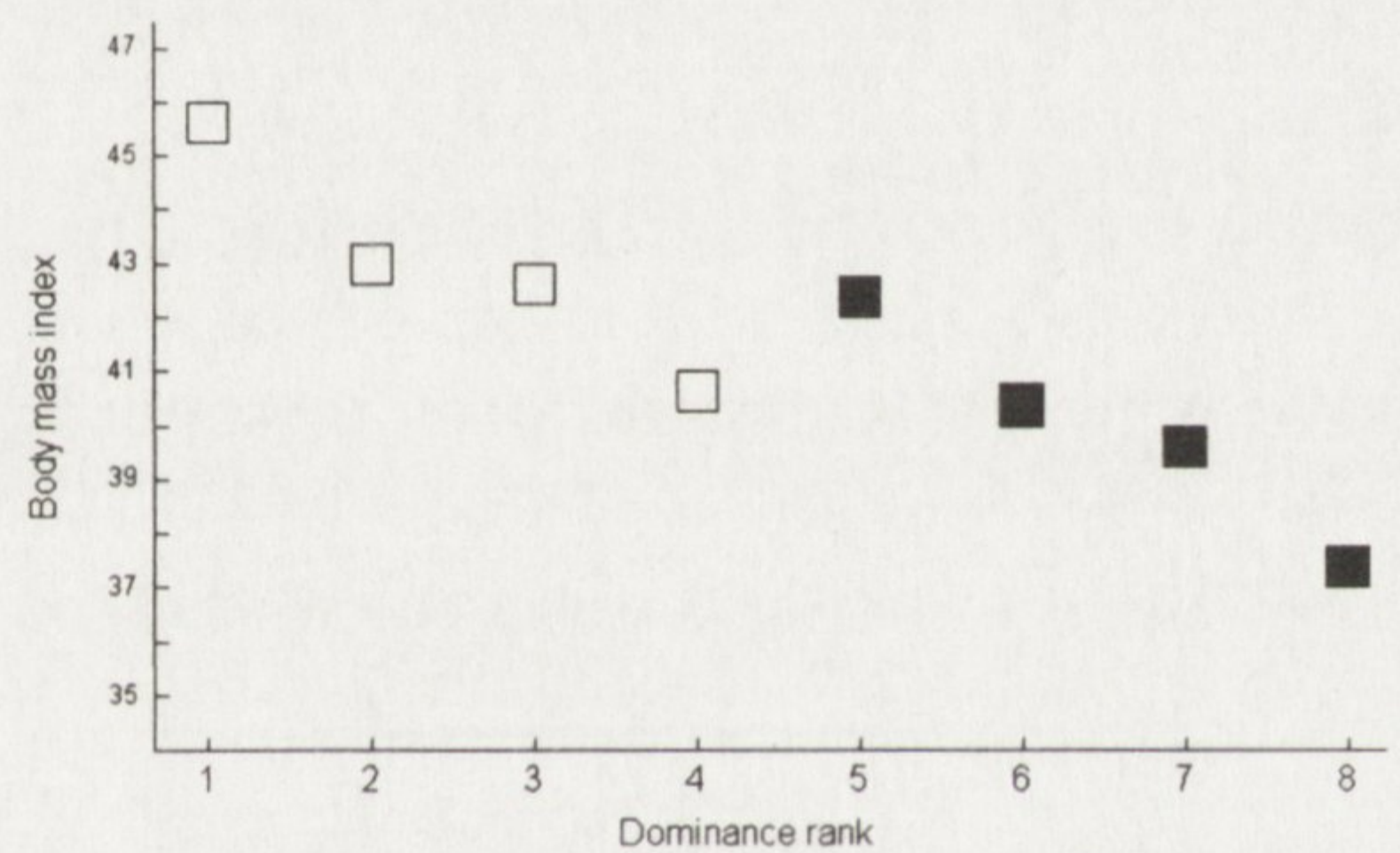


Fig. 1. Medians of body mass index (BMI) of willow tits (open square) and crested tits (filled square) in 10 mixed-species winter flocks relative to their dominance rankings (2-tailed Spearman rank correlation coefficient $r_s = -0.92$, $p = 0.014$). Top dominants were assigned a value of 8

Table 2. Body reserves of willow tits by rank and sex

	Males				Females			
	Dom.	Sub.	U	p	Dom.	Sub.	U	p
Body mass (g)	11.34	11.85	30	*	11.05	11.01	35	ns
SE	0.057	0.049			0.11	0.15		
BMI (kg/m^3)	40.8	42.9	24	**	43.0	45.5	17	**
SE	0.46	0.42			0.34	0.44		
Mean for CV of body mass of individuals	1.83	1.16		*	1.29	1.11		*
SE	0.29	0.33			0.19	0.22		
Number of individuals	10	16			10	13		

* $p < 0.05$, U-test, ** $p > 0.001$, U-test

Table 3. Body reserves of crested tits by rank and sex

	Males				Females			
	Dom.	Sub.	U	p	Dom.	Sub.	U	p
Body mass (g)	12.4	12.81	7	*	12.06	12.12	11	ns
SE	0.67	0.88			0.07	0.13		
BMI (kg/m ³)	37.3	39.9	3	***	40.5	42.4	4	**
SE	0.44	0.38			0.37	0.46		
Mean for CV of body mass of individuals	2.05	1.73		*	1.64	1.61		ns
SE	0.57	0.45			0.38	0.47		
Number of individuals	10	6			10	5		

* p 0.05, U-test, ** p 0.01, U-test, *** p 0.001, U-test

more stable evening body mass which is shown by the comparison of the coefficients of variation (Tables 2, 3). The coefficient of variation was calculated for

each individual separately and later the mean and standard error of such coefficients were calculated.

3.3. REMOVAL EXPERIMENT

To test whether the correlation between rank in a mixed-species flock and body reserves represents a causal relationship, I removed all of the crested tits in five groups. The remaining willow tits in experimental flocks rose in rank and became the only and dominant species. I compared them with willow tits in five unmanipulated flocks to control for seasonal effects on body reserves after re-

moval. I observed changes of BMI only in alpha individuals of the willow tit since they may increase access to the resources much more than their subordinate flock-mates.

The experiments confirmed a causal link between rank and the size of body reserves. Body mass index of five dominant willow tits decreased in response to removal of crested tits (Table 4) reaching

Table 4. The effect on body mass and body mass index of experimental subordinate willow tits from rising in rank after removal of crested tits and control willow tits with no change in rank

	Body mass	BMI	Individuals with significant response			
			+	0	-	p
Experimental subordinates	-0.55	1.67	0	0	5	*
SE	0.04	0.10				
n	5					
Control subordinates	-0.03	0.10	0	5	0	ns
SE	0.01	0.05				
n	5					

Distribution of responses in experimental and control group tested with binomial test, 1-tailed (direction predicted); * p < 0.05

the mean level of 40.97 kg/m^3 (U-test, $p > 0.01$) within a week (instead of 43.05 kg/m^3). The response was consistent

since body mass and fatness decreased significantly for all five experimental individuals of the willow tit (Table 4).

4. DISCUSSION

Within each 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 (Wilson 1975). In contrast, in comparisons of fatness where individual size was controlled for through body mass index, willow tits as a subordinate species carried larger body reserves. There is some previous evidence that the subordinate individuals accumulate larger body mass and fat reserves during their daily activity (Ekman and Lillendahl 1993). Willow tits and subordinate crested tits had larger fat reserves in spite of foraging difficulties in their feeding stations which as a rule are more exposed relative to predators (Ekman 1987, Suhonen 1993a, b, Krams 1996) and require, thus, more time for vigilance (Ekman 1987). The energetic costs in a subordinate time budget might conceivably be compensated by increased abundance of arthropods on small living twigs with needles in the outer parts in the coniferous tree canopy (Suhonen et al. 1992, Krams and Thiede, in press). However, the larger body mass accompanying more unpredictable access to food resources suggests that fat reserves are under control of a foraging strategy and is not simply constrained by food availability. This fattening policy of subordinate willow tits no doubt reduces probability of energetic shortfalls. Extra reserves of subordinate flock mates could be a buffer in times of increasing requirements, when dominants are likely to claim their prior-

ity of access to food (Ekman and Lillendahl 1993). This could be expected mainly during prolonged cold spells or severe winters. Not surprisingly, I found no starvation in willow tits as variations in winter temperature were small during my study. In contrast, all willow tit individuals carried larger fat reserves than dominating crested tits and the evening body mass of willow tits was less variable than that of crested tits. The relative variability of body mass and smaller fat reserves of crested tits could be explained rather by foraging predictability than the result of a cost of dominance (Hogstad 1987a) or starvation (Jansson et al. 1981). Otherwise, dominants with their small reserves would be exposed to a higher risk of energetic shortfall than subordinates. These facts apparently suggest that individuals of both tit species foraging optimally maintained a neutral energy balance regardless of rank.

In general, BMI gradually decreased by rank and sex from top-ranking crested tits to subordinate willow tits. In spite of one BMI overlap observed between an old willow tit male and a juvenile crested tit female, the results obtained suggest the influence of the dominant species individuals to the fattening strategies of their heterospecific flock-mates. The results of the removal experiment also confirmed the suggestion that deposition of energy reserves of willow tits was dependent on the presence of crested tits.

Although larger body reserves imply the risk of predation, willow tits in

mixed-species flocks probably enjoy more anti-predator protection due to the "many eyes" effect (e.g. Powell 1974, Ekman 1987). Considering a flock after removal of the crested tits, one can suggest two ways of how the remaining willow tits might increase their abilities to scan for the attacking predators. Firstly, the additional conspecific individuals might join the flock and, secondly, other heterospecific individuals such as other tit species, goldcrests (*Regulus regulus*) and treecreepers (*Certhia familiaris*) may join the remaining willow tits. According to the results of this study, the last case could increase the value of sociality, since heterospecifics as flock-mates do not affect the frequency of interference substantially. Further, interspecific encounters usually are milder than aggressive interactions among individuals belonging the same species. Still, assuming that one encounter between two heterospecific individuals gives a score for the both species involved, it gives two scores for a single species when an encounter occurs between two conspecifics. Thus, the presence of heterospecifics may mitigate intraspecific interference severity.

Aggressive behaviour is well documented in parids spending winter as members of non-kin social groups (e.g. Hinde 1952). By aggressive means dominant individuals realize their priority in access to the contested resources and punish subordinates. The use of time as a currency for trading costs and benefits is based here on the assumption that the use of time is important to fitness. Tits suffer energy stress in the short, cold days of

winter which appears to influence predator exposure (Jansson et al. 1981). Efficient use of time should then be of high survival value. It is also found that relatively more vigilant individuals enjoy an anti-predatory advantage over less vigilant group-mates suggesting a direct benefit of personal vigilance (Lima 1994, 1995). Agnostic encounters, decreasing time allocated to vigilance, therefore, may be costly for social individuals in terms of increased probability of successful attack by predator.

In conclusion, individual foragers in mixed-species groups can devote more time to feeding as group size increases without any increase in their personal risk of being preyed upon. Besides collective detection, foragers can enjoy benefits of their personal vigilance. The above effects are possible due to the decreasing frequency, intensity and duration of aggressive encounters among members of mixed-species flocks making heterospecific flocking to be the most beneficial and prevalent sociality form among parid species. Although physiological adaptive abilities in mixed-species groups are constrained by the presence of individuals of dominating species, social birds supposedly may increase their probability to survive till the next breeding season.

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5. SUMMARY

Efficient use of time is of high survival value for wintering parids whereas allocation of time either to anti-predator behaviour or

foraging may be dependent on tit flock composition. I studied the duration of interference interactions and changes in body mass

in response to the presence of heterospecifics in mixed-species flocks of free-living willow and crested tits. The study was done in pine forests of south-eastern Latvia. It was found that on the average intraspecific aggressive encounters are of longer duration than interspecific interactions (Table 1). Decreasing time allocated to intraspecific aggressiveness, social individuals in mixed-species flocks supposedly increase their probability of survival till the next breeding season. Social dependence of the two tit species was controlled by observations of their fattening strategies. Body reserves of willow tits as subordinate flock members were found to be

dependent on the presence of dominant crested tits (Table 1 and 2). Body reserves of members of mixed-species flocks negatively correlated with dominance rank within both intraspecific and interspecific hierarchies (Fig. 1). Removal experiments confirmed results of field observations, revealing a causal relationship between rank and ability to choose the safest fattening strategy (Table 4). Fattening strategies dependent on social status represent a flocking cost to individuals belonging to a subordinate species. However, increased foraging time may be considered as a benefit for all members of mixed-species flocks.

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