Does high social rank position affect winter survival of Willow Tits *Poecile montanus* negatively under prolonged conditions of extremely low ambient temperature?

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January 2010 was the coldest for more than 30 years in south Norway, with ambient temperatures in parts of central Norway between -30 and -40 ºC. The January survival rates of individually colour-ringed Willow Tits *Poecile montanus* were studied by comparing the numbers of survivors from 10 flocks under the extremely low ambient temperatures in 2010 with that of 8-9 flocks under milder conditions in the two previous years. All flocks consisted of an adult mated pair and two to four unrelated juveniles, and in the flock hierarchy males generally dominated the females and the adults dominated the juveniles of their own sex.

As expected, relatively fewer low-ranked juveniles survived January 2010 than in the previous years (0-20%, mean 13% vs 0-89%, mean 56%). But also the January survival rate of the top ranked males, the alpha birds, of the flocks in 2010 was lower (40%) than that during the two previous winters (88% and 89%). Because the top-ranked adult males have about 10% higher day-time oxygen consumption rates than the lower ranking birds in the same flock, the energetic requirements are higher for the alpha males than for the other flock members. This extra energy demand may have negatively influenced their survival during the long extremely cold period.

Key words: Winter survival, temperature stress, Willow Tit, *Poecile montanus*, social dominance

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INTRODUCTION

The Willow Tit *Poecile montanus* is a highly sedentary species, and most individuals live within flock territories outside the breeding season. Breeding pairs remain in their exclusive areas throughout the year. During the winter these areas are defended by small, non-kin flocks, formed as the roaming yearlings become sedentary and join the adults during the late summer and autumn. Once established, stable hierarchies are maintained in these flocks during the winter. The flocks consist most often of the adult mated pair and two juvenile males and two juvenile females (Ekman 1979, Hogstad 1987a) where the males generally dominate the females and the adults dominate the juveniles of their own sex (Hogstad 1987a).

During short and cold winter days, tits suffer from energy shortage (Jansson *et al*. 1981), and individuals with priority to food may gain survival benefits. Studies have demonstrated that adult Willow Tits survive the winter better than juveniles (Ekman *et al*. 1981, Ekman 1984, Hogstad 1989a), often because the dominant adults secure priority to resources (e.g. Ekman & Askenmo 1984, Pulliam & Caraco 1984, Hogstad 1988). Also high-ranking pairs of Black-capped

Chickadees *Parus atricapillus* survived significantly better than juvenile or lower-ranking pairs (Smith 1984).

January 2010 was extremely cold over most of the Southern Norway with long-lasting periods of temperatures between -30 and -40 ºC in parts of inland central Norway, being the coldest for more than 30 years (Norwegian Meteorological Institute; *www.met.no*).

I studied the survival rate of wintering Willow Tits in relation to their social dominance status under two contrasting temperature regimes: the cold January 2010 and the warmer January in the two previous years. Based on the knowledge of winter survival of the tits, it was hypothesised that the low-ranked juvenile flock members would suffer most and that the highest ranked least when exposed to the extremely low ambient temperatures.

METHODS

The study was carried out in a subalpine, mixed forest of Scots Pine *Pinus sylvestris* and Downy Birch *Betula odorata* in Budal, central Norway (62º50'N, 10º25'E; see Hogstad 1987a).

The tits were caught in September and October 2007-2009 and individually colour-ringed, sexed (Haftorn 1982, Hogstad 1987a) and aged (Laaksonen & Lehikoinen 1976). The size and composition of the flocks were determined on the basis of the degree of coherence observed among the birds (Ekman 1979) during the period October-December, and the hierarchical order of the individuals within each flock was determined by observing the outcomes (winners and losers) of agonistic encounters at feeders (Hogstad 1987a). Each flock studied consisted of one adult mated pair and one or two juvenile males (m_1 and m_2) and one or two juvenile females (f_1 and f_2). The adult male (M) was always the most dominant bird (dominance rank 1) and the two juvenile females always the least dominant (dominance ranks 5 and 6). The adult female (F) ranked between the juvenile males and the juvenile females (i. e. dominance rank 3 or 4). However, because the adult male apparently protect his mate from the juvenile male flock members (Hogstad 1992), the adult female may in periods (when foraging close to her mate) have about the same rank as her mate ($M \approx F > m_1 > m_2 > f_1 > f_2$).

Willow Tit flocks have in general a constant membership until midwinter when some tits disappear (Hogstad 1989b). As none of the tits that disappeared were later observed in adjacent areas, and since no new individuals appeared within the study area during the winter, losses of birds were considered as a result of mortality. The comparative January survival rates of the Willow Tits were found by comparing the initial number of flock members from 8-10 flocks in December with the numbers of survivors found in early February.

The mean ambient January temperature in the area in 2010 was 13.1 and 10.8 ºC lower than in 2008 and 2009, respectively. In 2010 the mean temperature deviated -7.4 ºC from the «normal» (the mean of 1961-1990), whereas the means of 2008 and 2009 deviated +5.7 ºC and +3.4 ºC, respectively (Table 1).

Table 1. Mean January temperature based on data from Røros meteorological station (about 50 km from the field area). The data are from Norwegian Meteorological Institute, www.met.no. *The «normal» is the mean of 1961-1990.*

Year	Mean ºC	Deviation from normal	Lowest minimum ºC
2008	-5.5	+5.7	-23.3
2009	-7.8	+3.4	-31.9
2010	-18.6	-7.4	-42.1

RESULTS

All flocks studied consisted of 4-6 birds at the end of December, and all flocks consisted of an adult pair (M-F), one juvenile male (m_1) and one juvenile female (f_1; Table 2). In addition, five of these flocks had a juvenile male (m_2) and three-six flocks had a juvenile female (f_2). The mean flock size of the flocks studied (4.9-5.1) did not differ between years.

As expected, the January 2010 survival of the most subordinate flock members was low, and the survival rates of m_2 (20%) and f_1 (20%) differed significantly from that of 2008 and 2009 combined (m_2: χ^2=5.0, df=1, p=0.025; f_1: χ^2=8.13, df=1, p=0.004). The survival rate of the lowest ranked flock member, the f_2, is generally low. Thus, none of this category survived January 2010 or January 2009 (Table 2).

The survival rate of the top-ranked male, the alpha male, was also significantly lower in 2010 (40%) compared to that of the two previous years (88% and 89%; χ^2=7.03, df=1, p=0.008; Table 2, Fig. 1).

The adult female (F) and the highest ranked of the juveniles (m_1) had the highest survival rates among the flock members in 2010 (60%), and did not differ from that of the previous years (75% and 78%; χ^2= 0.82-2.90, df=1, ns; Table 2). Thus, the flock members that apparently managed the extremely low ambient temperature relatively well, were among the highest in the social hierarchy below the top ranked male.

DISCUSSION

Energy stress and predation are probably the most likely factors causing for winter mortality in Willow Tits (Ekman 1984). However, dominant adults and subordinate juvenile Willow Tits are exposed to different selective pressures, and adults normally survive significantly better than juveniles (Ekman *et al*. 1981, Hogstad 1988a).

The relatively low winter survival rate of the top-ranked males in 2010 may to a large extent be explained by their high metabolic rate. The alpha Willow Tits have, during the day, a mean oxygen consumption that is about 10% higher than that of the lower ranking birds in the same flock (Hogstad 1987b). At night, however, social dominance rank does not influence the metabolic activity of the birds (Reinertsen & Hogstad 1994). A positive relationship between rank position in the flock and oxygen-consumption rate (r=0.86, p<0.027; Hogstad 1987b) clearly demonstrate that social dominance entails an extra energetic cost. Dominant individuals probably have higher energy requirements due to a more active territorial defence against neighbours, protection of the mate from attacks by juvenile male flock members (Hogstad 1992) and attempts to rescue the mate from being taken by predators (Alatalo & Helle 1990, Hogstad 1995). Since dominant Willow Tits gain the best access to the available food resources (Ekman 1984, Hogstad 1988), they normally have no difficulty in compensating for this extra energetic cost. However, during the prolonged conditions of extreme low ambient temperature this energy demand may have negatively influenced the survival for the top-ranked males.

The adult females (F) and the highest ranked juvenile males (m_1) had a relatively better survival rate (60%) than the other flock members. The metabolic rates of these birds are similar, but lower than that of the alpha males (Hogstad 1987b). Being protected by their mates, the adult females are generally involved in fewer dominance interactions than the other flock members and may allocate more of their time to foraging and less to vigilance against predators (Hogstad 1992).

Dominant as well as subdominant individuals depend for survival on the energy reserve that they have built up during a few hours of daylight. This reserve must last through the night since it is impossible to replenish it until the next day. Even small differences in the daily requirements of food may thus make a difference between live and death.

Table 2. Total number of flock members of eight, nine and ten winter flocks in December 2007, 2008 and 2009, respectively. Right: Number of flock members of the same flocks observed in the first days of February the following year, i.e. numbers that had survived January.

	Number of flock members						Survival Dec.-Febr. (percent)		
	December			February					
	2007	2008	2009	2008	2009	2010	07/08	08/09	09/10
Admale	8	9	10	7	8	4	88	89	40
Adfemale	8	9	10	6	7	6	75	78	60
$Juvmale_1$	8	9	10	7	8	6	88	89	60
$Juvmale_2$	5	5	5	4	4	1	80	80	20
$Juvfemale_1$	8	9	10	5	8	2	63	89	20
$Juvfemale_2$	4	3	6	1	0	0	25	0	0
Flock size	4-6	4-6	4-6						
Mean flock	5.1	4.9	5.0						

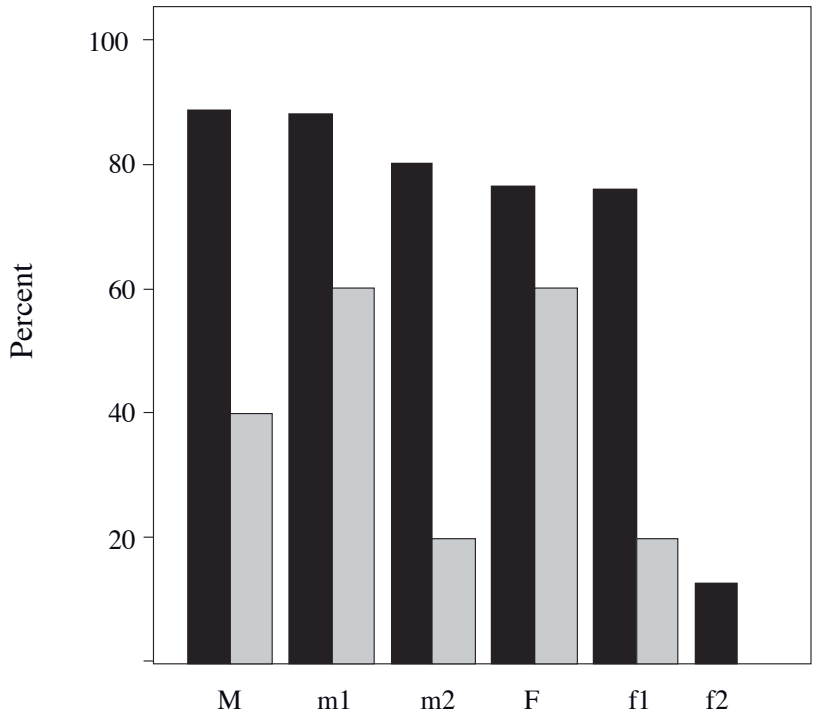

Figure 1. Mean percent survival rates of flock members of Willow Tits under mild conditions (January 2008 and 2009 pooled; black) and under extremely low ambient temperatures (January 2010; grey). The flock members are ordered according to their social rank position: Adult male (M, the alpha male) is the top ranked flock member (rank=1), the juvenile males (m_1 and m_2, ranks 2, 3), adult female (F, rank 4) and juvenile females (f_1 and f_2, ranks 5,6)

SAMMENDRAG

Kan høy sosial rang hos granmeis innvirke negativt på overlevelsen ved lange perioder med ekstremt lave temperaturer?

Januar 2010 var blant de kaldeste på mer enn 30 år i Sør-Norge. Nær undersøkelsesområdet i Budal, Sør-Trøndelag, var temperaturen i lange perioder mellom 30 og 40 kuldegrader. Jeg sammenliknet overlevelsen av granmeis gjennom januar 2010 (gjennomsnittstemperatur -18.6 °C) med januar de to foregående år (gj.sn. 2008: -5.5 °C; gj.sn. 2009: -7.8 °C). Fra tidligere er det kjent at gamle granmeiser overlever vinteren i klart større grad enn unge, i stor grad fordi de gamle er sosialt dominante og har bedre tilgang til prioriterte ressurser. Det ble derfor antatt at januarkulda i 2010 ville resultere i stor dødelighet blant de unge, mens de gamle meisene ville klare seg relativt bra.

Granmeisene er stedfaste og lever i vinterflokker på 4-6 individer. Flokken består av en territoriell eldre hann med make sammen med ett eller to unge par. Ingen er i slekt med hverandre. Innenfor flokken er det et sosialt hierarki hvor den gamle hannen, eller alfahannen, har høyest rang. Deretter kommer de unge hannene, den gamle hunnen og til slutt de unge hunnene.

Som forventet overlevde relativt færre lavt rangerte unge i januar 2010 (gj.sn. 13%) enn i januar de to foregående årene (gj.sn. 56%). Men også alfahannene hadde i gjennomsnitt en relativt lavere overlevelse i januar 2010 (40%) enn alfahanner i de to foregående årene (88% og 89%). Den høye dødeligheten av hannene øverst på rangstigen kan i stor grad skyldes ansvaret som følger «topplederjobben». På dagtid har alfahannen rundt 10% høyere stoffskifte enn de andre flokkmedlemmene. Han er mest aktiv, han må markere territoriet samtidig som han prøver å verne maken overfor rovfugler og konfrontasjoner fra unge hanner med høyere dominansstatus enn hunnen. Denne aktiviteten er energikrevende. Høy aktivitet i streng kulde øker behovet for mat for at stoffskiftet kan opprettholdes. Trolig taklet ikke alle alfahannene dette.

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