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Survival of Willow Tits *Poecile montanus*: the significance of flock membership, social rank and body size

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Abstract. The Willow Tit *Poecile montanus* is highly sedentary and 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 adults during late summer and autumn. Once established, stable social hierarchies are maintained in these flocks during the winter. The winter flocks consist normally of the socially dominant adult mated pair and two mated juvenile pairs, one higher-ranked and one lower-ranked. Here, individual Willow Tits, colour-ringed as juveniles in their first autumn in a subalpine forest in Norway, were followed till they disappeared. None of the lower ranked birds survived their first winter, whereas only 4 of 71 higher-ranked juvenile pairs disappeared during this time. Annual survival for dominant flock members was about 50% and similar for males and females. Thus, about half of the 71 pairs survived their first winter, about 25% survived two winters, 8.5% survived three winters, and 5.6% survived four winters. Alpha pairs remained mated and defended their common territory across years. Maximum age as revealed by ringing showed one female became six years old and two males ringed as adults were at least nine years old when last observed. The main factor associated with survival was early flock establishment that led to a high rank position among the juvenile flock members. Body size seemed insignificant. Birds that survived their first winter either succeeded in establishing as territory owners or they were forced into the role as floaters and probably perished.

Keywords: Social rank; winter survival; Willow Tit; parids

INTRODUCTION

Although the average life span of several parids is approximately 2.5 years (e.g. Smith 1991), some parids can live for a remarkably long time. Thus, the oldest ringed individuals of American chickadees (Clapp et al. 1983) and European tits (Cramp & Perrins 1993) were about ten years old, and Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major* even 12 and 15 years, respectively. During a long-term study of Willow Tits *Poecile montanus* in the Budal area in Norway, one individual which was at least 9.5 years old was recorded (Hogstad 2015a), the same as earlier found by Bakken et al. (2006).

It is generally accepted that among birds, the survivorship for individuals less than one year old is considerably lower than it is for older birds (e.g. Ekman 1984, Loery et al. 1987, Matthysen 1988, Hogstad1988a, 1989). The period after fledging is a dangerous time (Perrins 1965, Smith 1991), and the heaviest losses for Willow Tits probably occur when the juveniles have just left the nest and when the family breaks up and the juveniles leave the natal territory (Jansson et al. 1981, Ekman 1984, Hogstad 2014). Willow Tits are small passerines that maintain yearlong territories defended by a male and female mated pair. Outside the breeding season, the adult pair lives in a ´winter flock´ together with two to four unrelated first-year Willow Tits that have settled after a post-natal dispersal. Because Willow Tits live in a habitat that is largely saturated with dominant territory owners (Ekman 1989, Hogstad 1999), the juveniles are forced to stay as subordinate flock members in an occupied territory and hope for ownership. However, because the flock size apparently is limited (Hogstad 1989), and there are more fledglings produced than there are openings in winter flocks (Hogstad 1990a), a substantial proportion of juvenile Willow Tits does not achieve flock membership (Hogstad 2014). Establishment in such flocks seems crucial because an individual then strongly increases its probability of surviving the non-breeding season (Ekman et al. 1981, Hogstad 2013).

Here, individual Willow Tits, colour-ringed as juveniles in their first autumn in a subalpine forest in Norway, were followed till they disappeared. We studied survival in relation to flock membership, social rank order in the flock, body size, sex, and foraging and agonistic behaviour. Observations of foraging site section and associated agonistic behaviour have been published for a sub-sample of the study (Hogstad 2015b). Here we report results for such behaviours from the whole study period (1986–2014) because use of foraging sites may affect risk of predation (Hogstad 2015b).

MATERIAL AND METHODS

The study was carried out in a subalpine, mixed forest (altitude 600–750 m) composed of Scots Pine *Pinus sylvestris* and Downy Birch *Betula odorata* in Budal, in central Norway (ca 63°N), during 1999–2014. All the data were collected by OH. The most dangerous avian predators of Willow Tits in the area are Hawk Owl *Surnia ulula*, Sparrowhawk *Accipiter nisus*, Great Grey Shrike *Lanius excubitor* and Siberian Jay *Perisoreus infaustus*. The Willow Tits were caught in feeder-traps during July–October (mainly September–October) within a 5-km^2 area (from 2001 reduced to 3.5 km^2) and individually colour-ringed. This meant that the individual juvenile birds were followed from when they were 2–4 months old. The probability of detecting individual birds was high because of regular and frequent visits to the study area, including trapping at feeding stations and observations at the feeders and in the forests around. Willow Tits are quite tolerant to human presence (may easily be trained to feed from the hand). The subalpine forest is relative open, and the trees and bushes are not tall. In addition, few other birds are present in this habitat, in particular during autumn, winter and early spring.

When captured, wing length (maximum length), body mass and fat score were measured. Fat score was recorded by examining the visible subcutaneous fat content in the furculum of birds caught between 10:00 and 13:00, using a four-level scale (0 = no fat, 1 = a little fat, 2 = half full, 3 = full). Sex was determined by wing length, occasionally combined with body mass (to the nearest 0.2 g) (Haftorn1982, Hogstad 1987a). The birds were aged as juveniles (born in the same summer), or adults (born in the previous summer or earlier), by the shape and abrasion of the tail feathers (Laaksonen & Lehikoinen 1976). The size and composition of the flocks were determined on the basis of coherence (Ekman 1979) among the colour-ringed birds during July–October. Based on the mapping of movements and records of interactions among the winter flocks, approximate territorial borders could be determined. The average size of the territories was about 25 ha, similar to what has been found for Willow Tits elsewhere in Fennoscandia (Ekman 1979, Koivula & Orell 1988).

Dominance hierarchies within flocks were determined by observing winners and losers of interactions at feeders with sunflower seeds after the winter flocks had established. Four interaction types were considered: chasing, displacing, causing another bird to withdraw from the feeder, or waiting until another bird left the feeder (see Hogstad 1987a). Most winter flocks consisted of five or six members: an adult mated pair (M = male, F = female), and one or two juvenile males (m) and one or two juvenile females (f). As found earlier (e.g. Hogstad 1987a), the adult male was the alpha bird in all flocks and dominated both of the juvenile males which, in their turn, dominated all the females: M > m1 > m2 > F > f1 > f2. The juveniles were paired (m1 – f1, m2 – f2), and to our knowledge, all flock members were non-kin. In the present population of Willow Tits, the pair bond of the dominant pair seems to last for life. If one of the pair members dies, it is not necessarily replaced by one of the lower ranked juveniles; the juvenile pair may replace the widowed bird as a pair, as shown by a removal experiment (Hogstad 1999, 2015b).

To quantify the influence of adult (ringed prior to this study) presence on the foraging pattern of the juvenile flock members when the birds simultaneously visited a tree, their foraging height positions were recorded: lower (score 1) and upper (score 2) halves in pines, where the upper part presumably provided better protection from predators than the lower part (e.g. Hogstad 1988b). A total of 35 tits (14 adults and 21 juveniles) from 15 different flocks were observed at ambient temperatures below 0 °C in December–January. Only one record was made per individual per tree per day. Except from these data including adult birds, all Willow Tits analysed in the present study were juveniles.

In each of 15 years of the study, 12–18 juvenile Willow Tits were ringed in late summer or autumn. These birds, in total 230, were followed in the field until they disappeared. A total of 180 birds were members from 71 territorial flocks, whereas 50 birds were not members of any flock (later called floaters). Although we cannot rule out emigration as a cause of loss from the population, Willow Tits within the study population exhibited high site fidelity, and it is likely that when a bird disappeared from a flock, it had perished. As part of another field study, visits were also made outside the study area looking for ringed birds. Birds were considered to have survived the winter if they were seen in March or later in the year following ringing in autumn. In addition to these individuals, we describe the longevity of seven Willow Tits ringed in the study area and being older than five years, five ringed as juveniles and two ringed as adults.

RESULTS

Winter and annual survival

Four pairs of the socially dominant juvenile flock members (m1–f1), and 22 males (m2) and 18 females (f2) of the subordinate juvenile flock members, disappeared in early winter (November and December). None of the 50 floaters were observed after ringing, and none of the subordinate flock members (m2 and f2) survived their first winter (Table 1).

When considering only the socially dominant

Table 1. Number of socially dominant flock members (m1 and f1) of Willow Tits that survived their first winter and the subsequent 2–6 winters, and mean wing length (mm).

	Males (m1)				Females (f1)			
No. of winters	No. survived	(%)	Wing length Mean	SD	No. survived	(%)	Wing length Mean	SD
1	36	(50.7)	66.1	0.75	36	(50.7)	62.9	0.75
2	17	(23.9)	65.9	0.70	17	(23.9)	62.8	1.03
3	6	(8.5)	66.0	0.63	6	(8.5)	63.3	0.82
4	4	(5.6)	66.0	0.82	4	(5.6)	63.5	0.58
5	3	(4.2)	66.3	0.58	2	(2.8)	63.5	0.71
6	1	(1.4)	66.0	-	0	-	-	-

juvenile flock members (m1 - f1 pairs), half (36 of 71, 51%) of them survived between autumn and March–April the following year. The survival rate was similar for the next year (17 of 36 survived, 47%). Of the dominant flock members, about 25% of the 71 pair members survived two winters, whereas 8% or less survived more than two winters. One male (m1, 1.4%) of the flock members survived six winters, while none of the f1 females did so. Thus, annual survival was similar throughout life (about 50%), and similar for males and females. Of the seven cases of presumably unpaired Willow Tits older than five years, two males and one female reached an age of six years, two males seven years, and two males ringed as adults reached at least nine years.

Territorial pairs tended to remain on the same territory between years, most defending it until one of the mates died. No divorce among adults was recorded, whereas a few divorces occasionally did occur among the juveniles, all in response to the death of a member of an alpha pair. Although some pairs failed to reproduce due to nest predation, they still remained paired in the next breeding season. First-wintering m1 males that survived to March–April, tried to become established as territory owners, either by finding a vacant area or by gaining one by replacing the territorial owner. Those which failed were forced into the roles as floaters.

Foraging

During their first winter, juveniles frequently foraged together with the adult pair. When an adult and a juvenile simultaneously visited a tree, both dominant and subordinate juveniles foraged significantly more in the lower part of pine trees than did adults (juvenile relative height: 1.24; adults: 1.86 ($t = 4.39$, $df = 33$, $p < 0.001$).

Body size and fat score

Lower-ranking juvenile flock members were heavier than their dominant flock mates in males (m2: 12.3 g vs. m1: 12.1g; t - test, $t = 2.42$, $df = 18$, $p = 0.03$), but not in females ($t = 0.52$, $df = 18$, $p = 0.61$). Also mean fat score for lower-ranking males was greater than that for higher-ranking males ($t = 2.71$, $df = 13$, $p = 0.02$) but not for females ($t = 1.25$, $df = 13$, $p = 0.23$).

Thus, body size was apparently of minor significance for rank order in the winter flocks. No significant variation was found in wing length across the years for those which survived the winters (Table 1; One-Way ANOVA: males m1: $F_{6,70} = 0.28$, $p = 0.90$; females f1: $F_{5,68} = 1.23$, $p = 0.31$), nor between dominant and subordinate juvenile flock members or floaters (Table 2; One-Way ANOVA: males m1: $F_{2,118} = 2.74$, $p = 0.07$; females f1: $F_{2,110} = 1.86$, $p = 0.16$).

Territorial disputes and losses

As reported earlier, aggressive interactions were mainly found in two periods, namely in early autumn and in spring (Hogstad 2015b). Territorial males were observed fighting with intruding (unringed) Willow Tits that apparently challenged the owners, and it was usually males between 3–5 years old which were most involved (Table 3), probably because there were more males of these ages which were territorial. Occasionally, the adult pair accompanied by the juvenile flock members met one of the neighbouring territorial flocks at the border. This resulted in agonistic interactions, mainly between the alpha pairs of the flocks, but also between the juvenile flock members in some cases. Fights did not seem to cause mortality but apparently spending time and effort on such activity was not without a cost, in particular if the bird lost rank position.

Only two cases of replacement of territorial owners were recorded. One territorial mated pair that disappeared in April was replaced by unknown birds that achieved territory ownership. In the second case, an adult alpha female died in May and her mate disappeared about a week later. Then the higher-ranked juvenile flock members (m1 and f1) took over the dominant position of the alpha pair. Individuals of neighbouring

Table 2. Mean wing length (mm), body mass (g), and fat score (visible subcutaneous fat content in the furculum, scale 0 - 3) of juvenile flock members of Willow Tits (dominants m1 and f1, and subordinates m2 and f2) and of juvenile floaters (not flock members).

	Flock members						**Non-flock members**		
	Dominants (m1)			Subordinates (m2)			Floaters		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
Males									
Wing length	66.0	0.72	71	65.7	0.63	22	65.7	0.55	26
Body mass	12.1	0.18	11	12.3	0.14	9	-	-	-
Fat score	1.1	0.35	8	1.7	0.49	7	-	-	-
Females									
Wing length	63.0	0.82	69	62.6	1.04	18	62.7	0.62	24
Body mass	11.1	0.28	12	11.2	0.10	8	-	-	-
Fat score	1.0	0.50	9	1.3	0.52	6	-	-	-

flocks could be observed at feeding stations within the territory without being chased. However, then the intruders always behaved submissively.

DISCUSSION

Annual survival was about 50% for the adult Willow Tits which meant that only about 4% of birds survived five years. If we include seven Willow Tits ringed in the study area prior to this study, two males ringed as adults became at least nine years old. The survival of males and females was similar, as has been found for Willow Tits in Finland (Koivula & Orell 1988) and an average annual survival rate of about 50% is similar to that in several other passerines (Dobson 1987, Gosler 1993, Orell & Ojanen 1979, Matthysen 1988). The survival of juvenile Willow Tits during their first winter was dependent on early settlement in a winter flock. Juvenile males that settled early achieved a higher dominance rank than males that settled later (cf. Hogstad 1990b). Because membership in a flock during autumn apparently serves as an insurance to be allowed to stay in the local area during winter, selection may act on parents to make their young able to disperse and settle early (e.g. Nilsson 1990). None of the floaters were observed after ringing. As reflected in the high survival rate of the adult birds, this was hardly due to mortality caused by the ringing procedure. Because of the tolerance of Willow Tits to human presence, and the effort invested in tracking ringed birds, we do not think these birds simply escaped our attention.

In some studies, rank position in a flock is related to body size (Garnett 1981, Hogstad 1987a, Koivula et al. 1993) but the present results showed that in Willow Tits prior residency was more important than body size, as has been shown in many other studies of parids (e.g. Lehikoinen 1986, Nilsson 1990, Schubert et al. 2007, Pakanen et al. 2016). In contrast to body size (i.e. wing length), we found rank-related differences in body mass and fat score among male flock members. This is in accordance with the optimal body mass hypothesis (Slagsvold 1980, Lima 1986) suggesting that lower-ranked birds should carry more fat in a resource-limited environment during winter (e.g. Clark & Ekman 1995, Krams et al. 2010). Dominant individuals with better access to food need not depend on fat reserves to the same extent as subordinates. An increase in energy reserves may reduce the probability of starvation, whereas an increase in body mass may reduce the probability of successfully escaping a predator.

The mortality of Willow Tit flock-members in

Table 3. Age (number of winters) of territorial male Willow Tits observed fighting with an unmarked tit in February–April.

	Age of territorial male						
	1	2	3	4	5	6	Total
No. of fights	1	1	5	6	5	1	19

Budal during their first winter was strongly affected by the bird´s social rank. About 50% of the dominant juvenile m1–f1 pairs survived their first winter while none of the lower ranked birds did so. Low-ranked juveniles seem to be forced to forage in relatively dangerous microhabitats (Ekman & Askenmo 1984, Hogstad 1988b, Ekman 1986) and suffer increased predation risk, especially when energetic constraints are severe (Hogstad 1988b). Accordingly, rings of subordinate Willow Tits were more often found in prey remnants of the Pygmy Owl *Glaucidium passerinum* and of Northern Hawk Owl than those of dominant individuals (Ekman et al. 1981, Hogstad 1986). Because Sparrowhawks and small owls (Mikkola 1983, Hogstad 1986) often catch small birds from the lower branches of the trees, predation risk should be higher in the lower and outer parts of the trees (Ekman 1986). In addition to scanning for predators, subordinates must also be vigilant against dominant individuals. Thus, increased predation risk, and reduced foraging time, may be key factors causing the rank-dependent winter survival among the flock members (e.g. Ekman 1987, 1990, Desrochers 1989, Hogstad 1988 a,b). Also, Willow Tits store food and the food deposits may be used more by adults than by juveniles during winter.

First-year males that survived until March–April, tried to become established as territory owners, either by finding a vacant area or by replacing a territory owner. Failing birds were forced to adopt a floater or transient status with low chances of survival (Hogstad 2014). In social birds, an increased metabolic rate may be necessary to maintain a high rank position in a flock, and also to chase new intruders and defend the territory against neighbours (Hogstad 1987a,b). The effort may reduce the survival of the top-ranked males during prolonged periods of low ambient temperatures (e.g. Hogstad 2010). The ability to defend an alpha position declines with age in the Willow Tit, as it does in Great Tits (Dhondt 1985), with fighting success declining after the age of two years (Hogstad1999). Although a large body size may improve fighting ability in some birds (Koivula et al.1993) we did not find a relationship between survival and wing length in the present study.

To conclude, in juvenile Willow Tits, flock membership and rank position were the best predictors of survival. Higher-ranked flock members had greater winter survival than lower-ranked birds. Both members of the higher-ranked pairs were equally likely to survive to the breeding season. Because a wintering territory apparently provided a future breeding territory (Ekman 1990, Koivula et al. 1993), there is a strong selection for rapid settlement of the Willow Tits in winter flocks in the autumn (e.g. Hogstad 1990a).

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REFERENCES

Bakken, V., Runde, O. & Tjørve, E. 2006. Norsk ringmerkingsatlas. Vol. 2. Stavanger Museum, Stavanger.

Clapp, R.B., Klimkiewicz, M.K. & Futcher, A.G. 1983. Longevity records of North American birds: Columbidae through Paridae. J. Field Ornithol. 54: 123–137.

Clark, C.W. & Ekman, J. 1995. Dominant and subordinate fattening strategies: a dynamic game. Oikos 72: 205–212.

Cramp, S. & Perrins, C.M. 1993. Handbook of the Birds of the Western Palearctic. Vol. VII. Oxford University Press, Oxford.

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

Dhondt, A.A. 1985. Do old Great Tits forego breeding? Auk 102: 870–872.

Dobson, A.P. 1987. A comparison of seasonal and annual mortality for both sexes of fifteen species of common British birds. Ornis Scand. 18: 122–128.

Ekman, J. 1979. Coherence, composition and territories of winter social groups of Willow Tit *Parus montanus* and Crested Tit *P. cristatus*. Ornis Scand. 10: 56–68.

Ekman, J. 1984. Density-dependent seasonal mortality and population fluctuations of the temperate-zone Willow Tit (*Parus montanus*). J. Anim. Ecol. 53: 119–134.

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. Acta XIX Congr. Int. Ornithol.: 2373–2381.

Ekman, J. 1989. Group size in dominance-structured populations. Ornis Scand. 20: 86–88.

Ekman, J. 1990. Alliances in winter flocks of Willow Tits - effects of rank on survival on male-female associations. Behav. Ecol. Sociobiol. 26: 239–245.

Ekman, J. & Askenmo, C. 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 – a removal study. J. Anim. Ecol. 50: 1–9.

Garnett, M.C. 1981. Body size, its heritability and influence on juvenile survival among Great Tits, *Parus major.* Ibis 123: 31–41.

Gosler, A. 1993. The Great Tit. Hamlyn Species Guides. London.

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 norv. Ser. C, Cinclus 5: 16–26.

Hogstad, O. 1986. On the winter food of the Hawk Owl *Surnia ulula*. Fauna norv. Ser. C, Cinclus 7: 83–89.

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

Hogstad, O. 1987b. It is expensive to be dominant. The Auk

194: 333–336.
Hogstad, O. 1988a. Social rank and antipredator behaviour of Willow Tits *Parus montanus* in winter flocks. Ibis 130: 45 56.
Hogstad, O. 1988b. Rank-related resource access in winter flocks of Willow Tit *Parus montanus*. Ornis Scand. 19: 169–174.
Hogstad, O. 1989. Subordination in mixed-age bird flocks – a removal study. Ibis 131: 128–134.
Hogstad, O. 1990a. Winter floaters in Willow Tits *Parus montanus.* A matter of choice or making the best of a bad situation? Pp. 415–421 in Blondel, J. et al. (Eds.) Population Biology of Passerine Birds. Springer-Verlag, Berlin.
Hogstad, O.1990b. Dispersal date and settlement of juvenile Willow Tits *Parus montanus* in winter flocks. Fauna norv. Ser. C. Cinclus 13: 49–55.
Hogstad, O. 1999. Territory acquisition during winter by juvenile Willow Tits *Parus montanus*. Ibis 141: 615–620.
Hogstad, O. 2010. Does high social rank position affect winter survival of Willow Tits *Poecile montanus* negatively under prolonged conditions of extremely low ambient temperature? Ornis Norv. 33: 130–134.
Hogstad, O. 2013. Fattening strategies and social status in Willow Tits *Poecile montanus* during the non-breeding season: support for the optimal body mass hypothesis. Trans. R. Norw. Soc. Sci. Lett. 2013: 1–13.
Hogstad, O. 2014. Ecology and behaviour of winter floaters in a subalpine population of Willow Tits, *Poecile montanus.* Ornis Fenn. 91: 29–38.
Hogstad, O. 2015a. Granmeis (Willow Tit). Great Norwegian Encyclopedia.
Hogstad, O. 2015b. Rank-related response in foraging site selection and vigilance behaviour of a small passerine to different winter weather conditions. Ornis Fenn. 92:53–62.
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 Fenn. 65: 114–120.
Koivula, K., Lahti, K., Orell, M. & Rytkönen, S. 1993. Prior residency as a key determinant of social dominance in the Willow Tit (*Parus montanus*). Behav. Ecol. Sociobiol. 33: 283–287.
Krams, I., Cirule, D., Suraka, V., Krama, T., Rantala, M.J. & Ramey, G. 2010. Fattening strategies of wintering Great Tits support the optimal body mass hypothesis under conditions of extremely low ambient temperature. Func. Ecol. 24: 172–177.
Laaksonen, M. & Lehikoinen, E. 1976. Age determinations of Willow and Crested Tit *Parus montanus* and *P. cristatus*. Ornis Fenn. 53: 9–14.
Lehikoinen, E. 1986. Dependence of winter survival on size in the Great Tit *Parus major*. Ornis Fenn. 63: 10–16.
Lima, S. 1986. Predation risks and unpredictable feeding conditions: determinants of body mass in birds. Ecology 67: 377–385.
Loery, G., Pollock, K.H., Nichols, J.D. & Hines, J.E. 1987. Age-specificity of Black-capped Chickadee survival rates: analysis of capture-recapture data. Ecology 68: 1038–1044.
Matthysen, E. 1988. The Nuthatches. T & A D Poyser Ltd, London.
Mikkola, H. 1983. Owls of Europe. T. & A.D. Poyser, Calton.
Nilsson, J.-Å. 1990. Establishment success of experimentally delayed juvenile Marsh Tits *Parus palustris*. Ethology 85: 73–79.
Orell, M. & Ojanen, M. 1979. Mortality rates of the Great Tit *Parus major* in a northern population. Ardea 67: 130–133.
Pakanen, V.-M., Koivula, K., Orell, M. & Rytkönen, S. 2016. Sex-specific mortality costs of dispersal during the post-settlement stage promote male philopatry in a resident passerine. Behav. Ecol. Sociobiol. 70: 1727-1733.
Perrins, C.M. 1965. Population fluctuations and clutch size in the Great Tit *Parus major* L. J. Anim. Ecol. 34: 601–647.
Schubert, K.A., Mennill, D.J., Ramsay, S.M.,Otter, K.A., Boag, P.T. & Ratcliffe, L.M. 2007. Variation in social rank acquisition influences reproductive success in black-capped chickadees. Biol. J. Linn. Soc. 90: 85–95.
Slagsvold, T. 1980. Morphology of the Hooded Crow *Corvus corone cornix* in relation to locality, season, and year. Fauna norv. Ser. C, Cinclus 3: 16–35.
Smith, S.M. 1991. The Black-capped Chickadee. Cornell University Press, Ithaca and London.

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