

Growth and heritability of size traits of Willow Tit *Parus montanus* nestlings — a supplementary feeding experiment

Anna Thessing

Thessing, A., Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden; e-mail: anna.thessing@zoologi.su.se

Received 5 October 1998, accepted 25 January 1999



Growth and final body size of passerine birds may be influenced by both genetic and environmental factors, growth often being constrained by food limitation. This study investigates whether the growth of nestling Willow Tits *Parus montanus* is constrained due to food shortage and if offspring resemble their parents more in body size when parents are given access to additional amount of food (maggots). This was studied by comparing nestling growth in food-supplemented and control broods. During the study year nestling period coincided very well with peak abundance of caterpillars, the main prey of Willow Tits. This resulted in a very good growth of nestlings in the control group. Of the morphometric measurements, only wing length at 13 days of age differed between nestlings in fed broods and unfed controls. To control for the influence of heritable variation in growth a cross-fostering experiment was carried out with six broods. When eliminating the genetic factor, additional food showed a tendency to affect body mass at 13 days. The heritability of tarsus length was very high ($h^2 = 0.89 \pm 0.28$). It is proposed that fast growth rather than large body size *per se*, is a life history strategy enabling an early nest-leaving and early establishment as a member of a winter flock, which increases an individual's survival chances during the first winter.

1. Introduction

Growth of passerine birds may be influenced by both genetic and environmental factors. Selection will only lead to evolutionary change if a trait is heritable (Falconer 1989). Passerines have determinate growth, and in Willow Tits (*Parus montanus*) skeletal growth is completed just before fledging. Growth strategies may theoretically vary from a variable size with a growth period of fixed length to a fixed size but after an extended period of growth (Richner et al. 1989, Keller & van Noordwijk 1993). Environmental effects during the nestling period can influence both growth rate and

final body size (Boag 1987, Boutin 1990, Björklund 1992, Merilä 1997).

Willow Tits feed their nestlings mostly with caterpillars, which are available in high numbers for a short period in spring only (Kluyver 1951, van Balen 1973, Thessing in prep.). Hence, timing of reproduction to the caterpillar peak is crucial for nestling growth and later recruitment (Magrath 1991 & ref. therein). Willow Tits are territorial birds that form winter flocks of about four individuals with a strict social dominance hierarchy (Ekman 1979, Hogstad 1987, Koivula 1994, Lahti 1998). It may be advantageous for a juvenile to be large when establishing a territory in its

first year (Ekman 1979, Koivula et al. 1993), because of juvenile competition.

In an earlier study on Willow Tits the heritable component in tarsus length was estimated to be 0.62 and 0.82, respectively, in two different years (Thessing & Ekman 1994). In the year with the lower heritability, growth conditions were poor and there was selection in juveniles against short tarsus lengths. Birds selected against were small because poor growth had prevented them from reaching their body size potential. There was no selection on body size in the better year when all size classes were in good condition.

Experimental work on nestling growth has mostly compared growth in enlarged or reduced broods (Boutin 1990, Gebhardt-Heinrich & van Noordwijk 1991, Merilä 1997). To study growth potential and heritability without a food constraint, I offered Willow Tit parents maggots to feed their young with. Other researchers doing feeding experiments have been more interested in the parents' reaction during the pre-nestling period, notably in advance of the egg laying (Brömssen & Jansson 1980, Clamens & Isenmann 1989, Svensson & Nilsson 1995), clutch size, clutch asynchrony (Wiebe & Bortolotti 1995) or in future clutch sizes and other components of fitness (Nilsson 1990). There are few investigations of nestling growth rate in relation to additional food in a field experiment (but see Richner et al. 1989, Adams et al. 1994).

In this study, I investigate whether nestling growth rate is constrained because of food shortage, by manipulation of food abundance by additional food. I predicted that young would resemble their parents more in body size and get a higher heritability, when having access to additional food. To control for the parental environment, I did a cross-fostering experiment where I swapped chicks between additional fed and untreated nests.

2. Methods

2.1. Study area

The study area was around the Tovetorp Zoological Research Station in south-eastern Sweden (58°56'N, 17°08'E). This area is about 5 km² and consists of mixed coniferous woods with mostly

pine (*Pinus sylvestris*), but also spruce (*Picea abies*) and birch (*Betula sp.*). In the whole area there are about 200 nestboxes filled with wood shavings, mimicking a rotten trunk in which Willow Tits excavate a nest cavity. Nests in natural holes, often in a decaying birch, also occur in the study area. During 1995, 16 nests were built, both natural and in nestboxes, 13 of which were successful; two of the failing pairs successfully raised replacement broods which are included in the study.

2.2. Caterpillar abundance

In order to assess natural food abundance, I collected caterpillar faeces (frass) in three funnels with an upper area of 0.28 m² under each of five birches. The frass was collected in small paper bags, which were changed every third day, and later counted. All caterpillar excrements were counted independently of species.

2.3. Additional food experiment

In 1995 seven pairs of Willow Tits were offered about 25–50 g of maggots (*Tubellaris eristalis*) per day per brood, from the hatching day until fledging. The amount of maggots given was determined from calculations of maximum feeding rates. Parent Willow Tits feed their nestlings with a frequency of about once a minute, resulting in about 1 000 feeding visits in a sixteen hour day corresponding to 50 g of maggots. On a few occasions all maggots were gone when I brought new ones, but mostly about half the maggots remained when new maggots were to be supplied. For three pairs, maggots were placed near the nest (1–40 m) in enclosed seed-feeders, protected from jays (*Garrulus glandarius*) and woodpeckers (*Dendrocopos* spp.). These pairs were all used to feeding from feeders during the winter. Because it is very difficult to teach Willow Tits to use a new food source, the other pairs which were not used to feeders were given food in a camouflage-painted plastic pot placed on the nestbox, just under the entrance hole. Two nests had an automatic camera placed in front of the nestbox to be able to document what the parents were feeding

their nestlings with. For each nest 62% and 54% of the food items brought to the nestlings were maggots. Eight nests were untreated and served as controls, these correspond to "unfed" in the text.

2.4. Cross-fostering experiment

To investigate the influence of heritable (genetic) variation on the growth response of nestlings to additional food, I conducted a cross-fostering experiment with six of the broods, three of which had access to additional food and three of which were unfed (see also van Noordwijk 1989). I compared growth between siblings with and without extra food. When nestlings were 2–4 days old I swapped half the brood, three or four individual nestlings, between nests with the same number and age of nestlings and between fed and unfed nests. All clutches were of original size. I chose the nestlings by taking the first ones I picked up from the nest. In one brood, all but one nestling that had been transferred died before the age of ten days. These were excluded when analysing the cross fostering experiment.

2.5 Measurements of growth

In eleven out of the fifteen broods which were breeding in nestboxes, I weighed nestlings between the ages of 2–4, 6, 9, 11 and 13 days (hatching day as day 0) with an electric balance to the nearest 0.1 g. For individual identification, all the nestlings were individually marked with a nail-polish code on their claws. Tarsus length was measured to the closest 0.01 mm with callipers from the tarsus-tibiotarsus joint to the dorsal throchlea with the toes bent gently backwards. Wing length was measured with a ruler beginning at 6 or 9 days of age, when the feathers start emerging from the quill. Wings were measured to the nearest 0.5 mm, using the maximum wing length method (Svensson 1984). For nests in natural holes, I could measure the nestlings only once because of damage to the trunk and the disturbed reaction of the parents. These nestlings were estimated to be between 12 and 16 days old when measured, on the basis of their wing length. Hatch-

ing day was calculated for all broods by adding 14 days of incubation to the day when the last egg was laid. Around the calculated hatching day I checked the nests every or every second day. Hatching day for natural nests was controlled using a dentist's mirror or listening for newly hatched chicks. Parents which had not been caught and measured earlier, were mist netted at the nest when the nestlings were about 10–13 days old.

All treated and untreated nests were randomly chosen. Nests paired in the cross-fostering experiment had to have the same hatching date, to eliminate out-competing of nestlings due to different ages.

2.6. Statistics

Statistics were calculated with STATISTICA (1993). I predicted that nestlings fed with maggots would have faster growth and would be larger at fledging than unfed ones. Consequently, I used one-tailed tests when comparing the two treatments. The calculations were based on mean-values of home reared nestlings. Heritability was estimated from means of mid-parent/mid-brood regressions (Falconer 1989).

3. Results

3.1. Caterpillar abundance

After a spell of cold weather, even including temporary snow cover, caterpillars on birch emerged in the third week of May when the temperature rose drastically (about 20°C in one week). Simultaneously the first broods hatched and breeding was well timed to caterpillar occurrence (Fig. 1). Availability of natural food was unusually good during the nestling time (compare 1992 in Thesing & Ekman 1994).

3.2. Additional food experiment

At an age of 13 days or older, nestlings fed with maggots had significantly longer wings than unfed nestlings (Table 1). However, at the same age there were no significant differences, only a tendency,

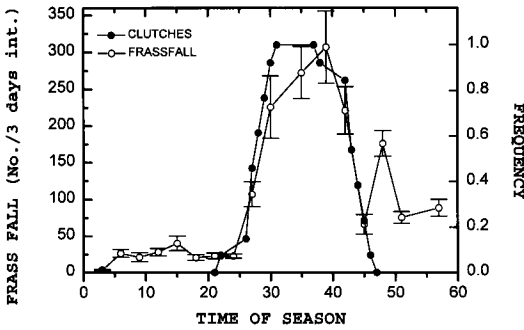


Fig. 1. Timing of nestling period and pattern of caterpillar abundance. Timing of nestling period: frequency of nests with nestlings (filled symbols). Seasonal distribution of caterpillar abundance as number of fallen frass during a three-day period (open symbols \pm S.E.). Time of season: days since 1 May.

for fed nestlings to have longer tarsi and to be heavier than unfed ones (Table 1). Except for wing length, growth had stopped at this age (Fig. 2a and b). This was confirmed when seven juveniles were recaptured in the autumn, three from “unfed” broods and four from maggot-fed broods; these birds had not increased in tarsus length (mean difference = - 0.08 mm, $t = - 1.17$, $df = 6$, $p = 0.26$, paired t-test). Earlier data on Willow Tit growth confirm this (Orell 1983, Thessing and Ekman 1994, Rytkönen et al. 1995). The growth curve for the wing is different because feathers will continue to grow (nearly 20 mm) after fledging (Fig. 2c).

3.3. Cross-fostering experiment

At the time of switching, there was no difference in body mass between siblings in treated and untreated groups (maggots fed = 2.5 g, unfed = 2.6 g,

paired t-test two-tailed $t = - 0.58$, $df = 5$, $p = 0.58$). No significant influence of switching was detected at an age of 13 days in either tarsus length (maggot fed \pm S.E = 18.51 ± 0.16 mm, unfed \pm S.E = 18.51 ± 0.09 mm, paired t-test $t = - 0.01$, $df = 4$, $p = 0.50$ one-tailed) or wing length (maggot fed \pm S.E = 39.9 ± 0.88 mm, unfed \pm S.E = 39.7 ± 0.89 mm, paired t-test, $t = - 0.19$, $df = 4$, $p = 0.43$ one-tailed). All siblings, except those originally from one nest, did grow equally or better in tarsus length with additional food (interaction in a 2-way ANOVA, $F_{(4,25)} = 1.30$, $p = 0.296$), but only siblings originally from one nest did have longer wings at this time (interaction in a 2-way ANOVA, wing length $F_{(4,25)} = 2.30$, $p = 0.087$). There was a tendency for siblings’ body mass to be higher if they had additional food (maggots fed \pm S.E = 11.7 ± 0.31 g, unfed \pm S.E = 11.2 ± 0.29 g, paired t-test $t = - 1.98$, $df = 4$, $p = 0.06$ one-tailed) and only siblings originally from one nest did not become heavier with additional food (interaction in a 2-way ANOVA, $F_{(4,25)} = 0.97$, $p = 0.443$).

3.4. Heritability

Heritability (\pm S.E.) for maggot fed nestlings was 1.66 ± 0.55 ($F_{(1,5)} = 9.11$, $p < 0.05$) and for unfed nestlings 0.53 ± 0.52 ($F_{(1,5)} = 1.05$, $p = 0.35$). The sample sizes are too small to draw conclusions about a difference between the two groups. Heritability for the pooled groups was 0.89 ± 0.28 ($F_{(1,12)} = 10.31$, $p < 0.01$), which is still rather high.

4. Discussion

Nestlings fed with maggots developed feathers faster than unfed ones and had longer wings at an

Table 1. Body size dimensions (\pm S.D.) at 13 days of age and mortality during nestling time. P is based on one tailed t-test (see methods), between maggots fed and unfed of home-reared nestlings.

	Pooled	Maggots fed	Unfed	p-value
Tarsus length (mm)	18.67 ± 0.38	18.82 ± 0.49	18.55 ± 0.19	0.09
Weight (g)	11.39 ± 0.42	11.54 ± 0.33	11.25 ± 0.47	0.09
Wing length (mm)	$39.47 \pm 3.15^*$	40.86 ± 2.50	$38.11 \pm 3.30^*$	0.05
Mortality	7.9% (7/89)	7.0% (3/43)	8.7% (4/46)	
n	15 (* n = 14)	7	8 (* n = 7)	

age of 13 days despite the small sample size and a "good year". There was also a tendency for additional food to have an effect on the final body mass or tarsus length of nestlings. The sample sizes are small and a power analysis for a type II error gives $(1 - \beta) = 0.40$ (60% chance for an accepted hypotheses of no difference to be false) for tarsus length and 0.38 for body mass (Dixon & Massey 1983). There was also a tendency for extra-fed nestlings to be heavier than unfed nestlings in the cross-fostering experiment, when genetic influence was controlled. The good availability of caterpillars, together with the very good timing of breeding is likely to have reduced the effect of additional food. Caterpillar development like this is not common (Fig. 1., Thessing in prep.). The cold weather during early spring caused delayed hatching in some clutches, which hatched about two days later than I expected. In that way, they synchronised even better with the caterpillar peak. It is likely that in normal years additional food has a larger effect.

The body condition (body weight/body size) of individual fledglings (nestlings at an age of 13 days) was generally good this year, probably because of good natural food availability. The body masses of all the fledglings were above a limit where survival chances appear to be good and only two individual nestlings (2.2%) had a body mass below 10 g, which is a very low frequency compared to other "good" or "rather good" years; 1992: 5.6%, 1993: 18.3%, 1996: 16.8% (pers. obs.). I believe 10 g is a threshold weight for good survival in Willow Tit fledglings, because Thessing and Ekman (1994) showed that those which were small were not in the same good condition as the large fledglings (tarsus length) and were selected against during the summer. The same phenomenon was seen in other poor growth years in this Willow Tit population such as 1990, 1994 and 1996 (Thessing in prep.). Even the mortality not due to predation was low. Only 8% of hatched nestlings died and the mortality occurred mostly after the age of 13 days and involved nestlings that hatched one or two days after the rest of the brood (Table 1). Those that died showed symptoms of attacks by parasites or had other indications of poor condition. This further indicates good food availability in this study.

The high heritability estimate for tarsus length

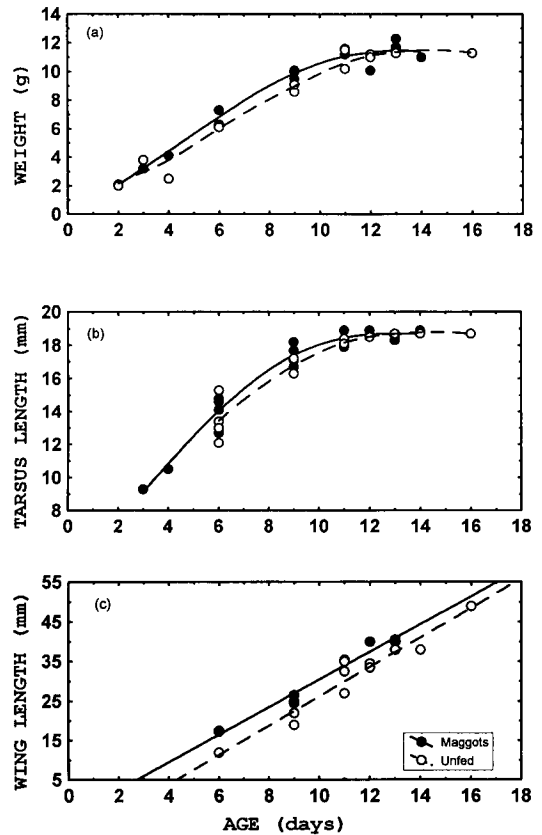


Fig. 2. Growth curves of (a) weight, (b) tarsus length and (c) wing length for broods with additional food (filled symbols) and without (open symbols). Brood means fitted with least square line (a and b) or regression line (c).

in Willow Tits might be caused by the benign growth conditions in 1995. Most other field studies have shown lower heritability for tarsus length (Song Sparrow *Melospiza melodia* $h^2 = 0.7-1.0$, Smith & Dhondt 1980; Blue Tit *P. caeruleus* $h^2 = 0.61$, Dhondt 1982; Pied Flycatcher *Ficedula hypoleuca* $h^2 = 0.53$, Alatalo & Lundberg 1986; Great Tit *Parus major* $h^2 = 0.52$, van Noordwijk et al. 1988; European Starling, *Sturnus vulgaris* $h^2 = 0.5$, Smith 1993). A high heritability means that almost all variance is explained by parental size, and environment has a lower influence (Falconer 1989). Several studies have shown a better growth in e.g., tarsus length with better quality or abundance of food and a higher h^2 (Boag 1987, Smith 1993, Merilä 1997). Life history traits are often phenotypically plastic and sensitive to food

availability (van Noordwijk et al. 1988, Boutin 1990). Because my sample sizes are small and the effect of additional food was small, I can not prove that heritability is lower during poorer growth conditions, though the pooled heritability is rather high and comparable with the high heritability in 1992, which also was a good year (Thessing & Ekman 1994).

In this study, maggot-fed nestlings had longer wings, which would enable them to fledge earlier and thereby increase their survival chances. Bjørnstad and Lifjeld (1996) found that the Willow Warbler (*Phylloscopus trochilus*) fledges later when nestlings were fed only by the female parent. The reason for the Willow Tits' greater wing length in this study could be coupled to an earlier start of development of feather growth. Growth of feathers usually has priority over other growth and follows a fixed schedule, it may even continue when nestlings starve (Boag 1987). Growth rate or time of growth is plastic, because maggot-fed nestlings had longer wings than the unfed at 13 days of age. A nest is at high predation risk, especially at the end of the nestling period, when energy demand is greatest and begging is noisy. In this situation, early fledging increases nestlings survival. Juveniles which have fledged early may also have a better chance of occupying an "empty" territory and later defending it from intruders (Ekman 1989, Nilsson 1990). It has been shown in earlier work on both birds and other taxa that possessors of territories have a better chance of retaining it than the intruders (e.g., Alcock 1975, Rand & Rand 1976, Leimar & Enquist 1984, Jakobsson 1988, Koivula et al. 1993). For juvenile Willow Tits, the time of settling in a territory could be important for the dominance order between regular flock members (Sandell & Smith 1991, Koivula 1994). Prior residency effects develop quite rapidly in Willow Tits and a few days are enough to make a bird dominant over a newcomer (Koivula et al. 1993). The differences in nestling time between the nests in this study were about a week (Fig. 1). Also, Glase (1973) showed that older juvenile Black-capped Chickadees (*P. atricapillus*) attained higher dominance positions in natural winter flocks, possibly because they arrived earlier in the area. Being a member of a flock may be more important even as a subordinate, because floaters have lower survival chances and

lower future rank in the flock than subordinate flock members (Ekman 1987, Koivula & Orell 1988). Early fledging in Willow Tits may be more important for survival and later reproduction than to be large *per se*, which is the case for several other bird species (e.g., Tinbergen & Boerlijst 1990, Magrath 1991).

In conclusion, additional food influenced the growth of Willow Tit nestlings, even though this effect was limited by the good availability of natural food this year. Extra-fed nestlings developed wing feathers faster and there was a tendency for higher body mass at an age of 13 days after genetic variation had been controlled for. It is most likely that faster growth during good food conditions is a life history strategy which enables Willow Tits to be an early fledgling, advantageous both for survival during the first winter and for later reproduction.

Acknowledgements: I thank Anders Bylin and Nils Andbjer for help in the field. Jan Ekman, Birgitta Tullberg, Markku Orell, Jack Windig and an anonymous referee gave me valuable comments on earlier drafts of this manuscript. This study was supported by grants from the Swedish Royal Academy of Sciences (Hierta-Retzius Foundation).

Sammanfattning: Tillväxt och ärftlighet av storlekskaraktärer hos talltite, *Parus montanus*, ungar — ett försök med tillskottsfoder

Tillväxten och slutlig storlek styrs hos tättingar både av genetiska och miljömässiga faktorer och den är ofta födobegränsad. Den här studien undersöker om Talltite (*Parus montanus*) ungar är begränsade av födan och om de kommer att likna sina föräldrar mer om de får obegränsat med föda under tillväxten. Detta undersöktes genom att titta på tillväxten där några kullar erbjöds extra mat (maggots) och jämfördes med kontroll kullar. Under försöksåret sammanföll häckningen väldigt väl med maximala mängden larver, talltitans huvudföda. Detta resulterade i en väldigt bra tillväxt även för ungarna i kontroll gruppen. Av de morfologiska karaktärerna (tarslängd, vinglängd och vikt) som undersöktes var det bara vinglängden som skilde sig statistiskt vid 13 dagars ålder mellan de

som fått extra mat och kontroll gruppen. För att kontrollera för den ärftliga variationen i tillväxt gjordes ett utbytes försök, där hälften av ungarna i sex kullar fick växa upp i ett annat bo. När man bortsåg från den genetiska faktorn, tenderade extra födan att ge en effekt på kroppsvikten vid 13 dagars ålder. Generellt var heritabiliteten var väldigt hög ($h^2 = 0.89 \pm 0.28$), vilket ytterligare visar på en låg miljömässig inverkan på kvantitativa egenskaper. Det föreslås att en snabb tillväxt i stället för en stor kropp är en livshistorie-strategi vilket leder till en tidig utflyttning från boet och ett tidigt etablerande i en vinterflock, vilket ökar överlevnads chansen under den första vintern.

References

- Adams, J. S., Knight, R. L., McEwen, L. C. & George, T. L. 1994: Survival and growth of nestling Vesper Sparrows exposed to experimental food reductions. — *Condor* 96: 739–748.
- Alatalo, R. V. & Lundberg, A. 1986: Heritability and selection on tarsus length in the pied flycatcher (*Ficedula hypoleuca*). — *Evolution* 40: 574–583.
- Alcock, J. 1975: Territorial behaviour by males of *Philanthus multimaculatus* (Hymenoptera: Sphecidae) with a review of territoriality in male Sphecids. — *Animal Behaviour* 23: 889–895.
- Balen van, J. H. 1973: A comparative study of the breeding ecology of the Great Tit, *Parus major*, in different habitats. — *Ardea* 61: 1–93.
- Björklund, M. 1992: Selection of bill size proportions in the Common Rosefinch (*Carpodacus erythrinus*). — *Auk* 109: 637–642.
- Bjørnstad, G. & Lifjeld J. T. 1996: Male parental care promotes early fledging in an open-nester, the Willow Warbler *Phylloscopus trochilus*. — *Ibis* 138: 229–235.
- Boag, P. T. 1987: Effects of nestling diet in growth and adult size of Zebra Finches (*Poephila guittata*). — *Auk* 104: 155–166.
- Boutin, S. 1990: Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. — *Can. J. Zool.* 68: 203–220.
- Brömssen von, A. & Jansson, C. 1980: Effects of food addition to Willow Tit *Parus montanus* and Crested tit *P. cristatus* at the time of breeding. — *Ornis Scand* 11: 173–178.
- Clamens, A. & Isenmann, P. 1989: Effect of supplemental food on the breeding of Blue and Great Tits in Mediterranean habitats. — *Ornis. Scand* 20: 36–42.
- Dhondt, A. A. 1982: Heritability of blue tit tarsus length from normal and cross-fostered broods. — *Evolution* 36: 418–419.
- Dixon, W. J. & Massey, F. J. 1983: Introduction to statistical analysis. 4th edition. — McGraw-Hill, Singapore.
- 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. 1987: Exposure and time use in willow tit flocks: the cost of subordination. — *Animal Behaviour* 35: 445–452.
- Ekman, J. 1989: Subordination costs and group territoriality in wintering Willow Tits. — *Proc. XIX Int. Ornithol. Congr.* 2373–2381.
- Ekman, J. 1990: Alliances in winter flocks of Willow Tits; effects of rank on survival and reproductive success in male-female associations. — *Behav. Ecol. Sociobiol.* 26: 239–245.
- Falconer, D. S. 1989: Introduction to quantitative genetics. 3rd edition. — Longman, Essex.
- Gebhardt-Heinrich, S. G. & van Noordwijk, A. J. 1991: Nestling growth in the great tit 1. Heritability estimates under different environmental conditions. — *J. Evol. Biol.* 3: 341–362.
- Gebhardt-Heinrich, S. G. & van Noordwijk, A. J. 1994: The genetical ecology of nestling growth in the Great Tit. Environmental influences on the expression of genetic variances during growth. — *Functional Ecology* 8: 469–476.
- Glase, J. C. 1973: Ecology of social organisation in the Black-capped Chickadee. — *The Living Bird* 12: 235–267.
- Hogstad, O. 1987: Social rank in winter flocks of Willow Tits *Parus montanus*. — *Ibis* 129: 1–9.
- Jakobsson, S. 1988: Territorial fidelity of willow warbler (*Phylloscopus trochilus*) males and success in competition over territories. — *Behav. Ecol. Sociobiol.* 22: 79–84.
- Keller, L. F. & van Noordwijk, A. J. 1993: A method to isolate environmental effects on nestling growth, illustrated with examples from the great tit (*Parus major*). — *Functional Ecology* 7: 493–502.
- Kluyver, H. N. 1951: The population ecology of the Great Tit, *Parus m. major*. — *Ardea* 46: 91–124.
- Koivula, K. 1994: Social dominance in Willow Tit (*Parus montanus*) flocks. — PhD dissertation, University of Oulu, Oulu, Finland.
- 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., Orell, M., & Rytönen, S. 1993: Prior residency as a key determinant of social dominance in the Willow Tit (*Parus montanus*). — *Behav. Ecol. Sociobiol.* 33: 283–287.
- Lahti, K. 1998: Social dominance and survival in flocking passerine birds: a review with an emphasis on the Willow Tit *Parus montanus*. — *Ornis Fennica* 75: 1–18.
- Leimar, O. & Enquist, M. 1984: Effects of asymmetries in owner-intruder conflict. — *J. Theor. Biol.* 111: 475–491.

- Magrath, R. D. 1991: Nestling weight and juvenile survival in the blackbird, *Turdus merula*. — *J. Animal Ecology* 60: 335–351.
- Merilä, J. 1997: Expression of genetic variation in body size of the Collard Flycatcher under different environmental conditions. — *Evolution* 51: 526–536.
- Nilsson, J.-Å. 1990: Establishment success of experimentally delayed juvenile marsh tits, *Parus palustris*. — *Ethology* 85: 73–79.
- Noordwijk van, A. J. 1989: Reaction norms in genetical ecology. — *BioScience* 39: 453–458.
- Noordwijk van, A. J., Balen van, J. H. & Scharloo, W. 1988: Heritability of body size in a natural population of the Great Tit (*Parus major*) and its relation to age and environmental conditions during growth. — *Genet. Res.* 51: 149–162.
- Orell, M. 1983: Nestling growth in the Great Tit *Parus major* and Willow Tit *P. montanus*. — *Ornis Fennica* 60: 65–82.
- Rand, W. R. & Rand A. S. 1976: Agonistic behavior in nesting iguanas: A stochastic analysis of dispute settlement dominated by the minimization of energy cost. — *Z. Tierpsychol.* 40: 279–299.
- Richner, H., Schneider, P. & Stirnimann, H. 1989: Life-history consequences of growth rate depression: an experimental study on carrion crows (*Corvus corone corone* L.). — *Functional Ecology* 3: 617–624.
- Rytkönen, S., Orell, M., Koivola K. & Soppela M. 1995: Correlation between two components of parental investment: nest defence intensity and nestling provisioning effort of Willow Tits. — *Oecologia* 104: 386–393.
- Sandell, M. & Smith, H.G. 1991: Dominance, prior occupancy, and winter residency in the great tit (*Parus major*). — *Behav. Ecol. Sociobiol.* 29: 147–152.
- Smith, H. G. 1993: Heritability of tarsus length in cross-fostered broods of the European starling (*Sturnus vulgaris*). — *Hereditas* 71: 318–322.
- Smith, J. N. M. & Dhondt, A. A. 1980: Experimental confirmation of the heritable morphological variation in a natural population of Song Sparrows. — *Evolution* 34: 1155–1158.
- STATISTICA 1993: Statistica for Windows, 4.2. — Stat-Soft Inc.
- Svensson, L. 1984: Identification guide to European Passerines. — Privately published, Stockholm.
- Svensson, E. & Nilsson, J.-Å. 1995: Food supply, territory quality and reproductive timing in the Blue Tit (*Parus caeruleus*). — *Ecology* 76: 1804–1812.
- Thessing, A. & Ekman, J. 1994: Selection on the genetical and environmental components of tarsal growth in juvenile Willow Tits (*Parus montanus*). — *J. Evol. Biol.* 7: 713–726.
- Tinbergen, J. M. & Boerlijst, M. C. 1990: Nestling weight and survival in individual great tits (*Parus major*). — *J. Anim. Ecol.* 59: 1113–1127.
- Wiebe, K. L. & Bortolotti, G. R. 1995: Food-dependent benefits of hatching asynchrony in American kestrels *Falco sparverius*. — *Behav. Ecol. Sociobiol.* 36: 49–57.