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Social dominance and survival in flocking passerine birds: a review with an emphasis on the Willow Tit *Parus montanus*

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Many birds spend the non-breeding season in flocks which exhibit a clear social hierarchy. This review outlines survival of passerine birds which live in such flocks. Survival is examined in relation to social dominance and to differences in behavioural patterns which may be associated with differences in survival probability. This paper has an emphasis on *Parus* species and especially on the Willow Tit (*P. montanus*) which is becoming a model species as far as the non-breeding season is concerned. Social dominance is viewed here as a relative measurement, not as a fixed property of an individual. One individual, the dominant, is typically defined as consistently having priority to access resources over another individual, the subordinate. This review concentrates on the following subjects: (1) The social organization of winter flocks; (2) Social influences on food caching; (3) The activity times of dominants and subordinates in relation to predator-risky times; and (4) The timing of mortality and importance of food on survival in dominance-structured flocks. Moreover, the seemingly paradoxical winter sociality is discussed: why do subordinate birds stay in flocks even though they are less likely to survive winter than dominants?

1. Introduction

1.1. General background

Behaviour is thought to be constantly optimised decision-making by individuals, balancing between the benefits and costs of the current context (Krebs & Davies 1991). One such decision is whether to aggregate with others. Forming a group offers many benefits, for example increased protection from predators and enhanced food finding (Bertram 1978, Pulliam & Caraco 1984). On the other hand, there are costs associated with grouping, e.g. increased fighting with others, and faster depletion of food by many mouths. However, the benefits and costs may not be the same for all group members (Rohwer & Ewald 1981, Ekman 1987).

1.2. Group life or solitude?

Although many species are strictly territorial during the breeding season, they spend the winter in stable, non-kin groups exhibiting dominance hierarchies (e.g. Matthysen 1990). During the winter the group members compete over resources in contests that are clearly asymmetric: dominants do well while subordinates do not. The fitness of dominants is typically greater than that of subordinates, since usually only individuals of high status breed (e.g. Dewsbury 1982). [Here, fitness is understood so that selection favours organs and behaviour which cause the individual's genes to be passed on (Dawkins 1982).] This seeming paradox raises a few questions. Why do low-ranking individuals stay in the group, when others are not even relatives? How can this behaviour persist? The search for answers to these questions makes the evolution of sociality an interesting object of investigation.

1.3. Social dominance

The literature about social dominance is enormous (Wilson 1975, Bernstein 1981). The concept of social dominance is, however, very heterogeneous. The word "dominance" is used for describing the competitive asymmetry in a variety of social systems. For example, in the caste system of social insects, the queen always dominates the workers, while in a highly complicated system of a primate society, the dominance relationship may suddenly change depending on e.g. the contested resource (Huntingford & Turner 1987). Many definitions link social dominance with aggression (e.g. Wilson 1975). Previously, aggression was commonly thought to be needed to maintain and advertise a dominant position. Later, it has been found that the subordinate individual often submits behaviourally to the dominant and thus accepts the dominant status of the other without aggression, individual recognition and memory being important during agonistic encounters (Hand 1986, Huntingford & Turner 1987, Drews 1993).

In the studies reviewed here, dominance status refers to dyads where one individual consistently has priority of access to resources and is called the dominant, while the other is subordinate by status. Rank refers to the position in a dominance hierarchy and may be high or low. Therefore, rank depends on group composition (Drews 1993). This paper views social dominance as a relative measurement, not as an absolute and fixed characteristic of an individual. The dominance relations may depend on the social context, site or time (Kaufman 1983, Hand 1986, Drews 1993; see also Bernstein 1981, Dewsbury 1982). Priority to food access has often been used as the definition of dominance in studies on birds, and this priority is presumed to describe an individual's general competitive ability. In a group with a linear hierarchy, as in a winter flock of tits (*Parus* spp.), the top-ranking individual dominates all the individuals below it in the hierarchy (Wilson 1975). Each step in the hierarchy is occupied by only one individual. The reader is advised to consult Drews (1993) for a thorough review on different definitions of dominance and the ordinal and nominal nature of the definitions.

1.4. Adaptations to life in winter

Sedentary animals in strongly seasonal regions have several adaptations to cope with the harsh winter with unpredictably varying conditions (cf. Levin et al. 1984). Change in colour or the thickness of fur or feathers improves camouflage or insulation. In addition to these kinds of morphological adaptations, animals can change their behaviour to enhance the probability of survival. Small northern birds for example may weigh more in winter than in other seasons (winter fattening) to hedge against colder weather and more unpredictable feeding conditions. They also increase their body mass by about 10% from morning to evening during the short winter day (daily accumulation of internal reserves) to be used the following night (Blem 1990, Witter & Cuthill 1993, Biebach 1996, Cuthill & Houston 1997). In the night, actively regulated hypothermia may help the individual save energy (Reinertsen 1996). However, hypothermia is not used always, perhaps because it increases reaction times and thus makes a hypothermic bird vulnerable to nocturnal predators (Grubb & Pravosudov 1994). Since fattening strategies and nocturnal hypothermia have been recently reviewed by several writers (see above), I shall not concentrate on these issues in this paper.

Intensive hoarding in autumn may postpone the availability of seasonally abundant food until lean times in winter (Vander Wall 1990). Caching by birds has been known for long: the earliest accurate descriptions of the behaviour date back to the 18th century (Sherry 1989). Until quite recently, food storing was believed to be communal in scatter hoarding species inhabiting nonexclusive territories (e.g. winter flocks of *Parus*). In the 1960s and 1970s, the benefit of hoarding to the individual hoarder was easy to envisage for some species which have precise memory of the location of each cache or defend it against others (Vander Wall 1990). However, the study of hoarding boosted only after Andersson and Krebs' (1978) influential paper, where hoarding as an evolutionarily stable strategy (ESS) in group-living animals was investigated. Andersson and Krebs listed two mechanisms which can make caching an ESS in a group: memory and individual niche specialisation may be used to recover more of their own caches than any other group member. These have, indeed, been found in later studies (e.g. Sherry 1989, Brodin 1994). The quest for possible cheater strategies and the influence of social context on hoarding have also received increasing attention lately (Vander Wall 1990, Bednekoff & Balda 1996).

1.5. The objectives

This review investigates survival of passerine birds living in groups, in relation to social status and differences in behaviour which may give rise to differences in survival. This paper has a special emphasis on the Paridae and especially on the Willow Tit (*Parus montanus*) which is to an increasing extent becoming a model species, as far as the non-breeding season is concerned. First, I describe the social system of free-living winter flocks and some consequences of dominance to different flock members. Then, I examine social influences and the effect of status on food hoarding. Does the presence of others affect the decision whether or where to cache? Which microhabitat do the birds store into? I also study the length of the daily activity period and survival of individuals of differing status in presumably time-limited conditions during short and cold winter days. What is the importance of food in determining how long a bird remains active during the day? Finally, I investigate the timing of mortality and significance of food on survival in dominance-structured flocks.

2. Hierarchy in winter flocks

2.1. Group structure

Sedentary passerine birds often live in social units in winter (e.g. Haftorn 1956, Kikkawa 1980, Schneider 1984). Several of these flocking species spend the winter in small, coherent and dominance-structured flocks and are territorial at that time (e.g. Smith 1976, Ekman 1979a, Waite 1987, Enoksson 1988; but see Smith & Van Buskirk 1988). The genus *Parus* is especially well studied in this respect (Hogstad 1989a, Matthysen 1990). In this genus, the constancy of the winter flocks ranges from permanent groups to temporary aggregations (Matthysen 1990). The Willow Tit belongs to the former group. Willow Tit flocks often consist of an adult pair which has bred in the same area in the preceding summer, with two to four probably paired, not closely related yearlings joining them (Ekman 1979a, Hogstad 1987a, 1988a, Koivula & Orell 1988, Haftorn 1990, Lahti et al. 1996). However, it is not uncommon that more than two adults spend the winter in the same flock (Haftorn 1990, Lahti et al. 1996). Immigrating yearlings settle in permanent winter flocks usually in August–mid-September (Koivula 1994, Haftorn 1997).

The average flock size of Willow Tits in northern Finland is 4.8 (746 birds in 154 flocks; Koivula & Orell 1988, Lahti et al. 1994, 1996, K. Lahti & K. Koivula, unpubl.). This falls in between the flock size of about four found in southern Sweden (Ekman 1979a) and in spruce-dominated areas of central Norway (Hogstad 1988a), and the flock size of six in subalpine regions in Norway (Hogstad 1987a). In eastern Siberia, Willow Tit flocks may be even larger (7–12; V. V. Pravosudov, pers. comm.), while in central Europe Willow Tits usually move in pairs (Ludescher 1973).

Improved protection from predators depends on group size, so that individuals in large groups are better protected, for instance due to increased probability of predator detection and decreased probability of being predated upon (Bertram 1978, Pulliam & Caraco 1984, Elgar 1989, Roberts 1996). Heterospecific birds join Willow Tits only occasionally in northern Finland (Koivula & Orell 1988, Lahti et al. 1996). Therefore, it does not seem likely that the flock size is lower there than in subalpine areas of Norway as the result of other species in the flock (cf. Hogstad 1988a). Northern Willow Tit flocks may be smaller than southern or eastern ones, due to smaller predation pressure so that small flocks are protected enough, or due to more scarce food resources which prevent flock size from increasing. Further south, in central Europe, with warm winters and more food than in the north, the food searching pressure of the birds might be more relaxed, so that flock size of two may be optimal. There, the "flock" can consist of paired birds which thus are actually territorial throughout the year (cf. Ludescher 1973). The sex ratio in Willow Tit flocks is typically equal and similar in different years, suggesting that the flock is composed of paired birds (Ekman 1979a, Hogstad 1987a, Haftorn 1990, Lahti et al. 1996).

There is variation in the average Willow Tit flock size between years in northern Finland, from less than four to more than five (Koivula & Orell 1988, Lahti & Rytkönen 1996, Lahti et al. 1996, 1997, K. Lahti & K. Koivula, unpubl.). Warm weather in late summer seems to be associated with large flock size, since the mean temperature in August and average flock size are significantly positively correlated (Spearman rank correlation, $r_s = 0.794$, $N = 10$, $P = 0.006$; data from Oulu, northern Finland, 1986–1993 and 1995–1997). No significant correlation was found between flock size and mean temperature in July ($r_s = 0.018$, $N = 10$, $P = 0.96$). This is intuitively plausible, because in July many Willow Tit juveniles are still within the family flocks and only then start to leave their natal territories (Haftorn 1997). Moreover, weather conditions just after the juveniles reach their independence, i.e. in late summer, may be more crucial.

It is probably the same factors that affect group size, both between different geographical areas and between years in the same area. However, analysing flock size determination in different areas is not possible due to lack of detailed information on e.g. variation in flock size between years or presence of other species in winter flocks. The interaction of habitat quality, competitive asymmetry between group members, and individual benefits contribute to determining the group size of dominance-structured flocks (e.g. Ekman 1989). Good habitats, as well as good years, can support bigger flocks than poor ones. Strong competitors may be more likely than weak ones to gain a position in a flock. For example, when there are more adults alive in autumn than there are available winter flock territories, it may pay off for the adults to flock together (Haftorn 1990, Lahti et al. 1996). This may further leave fewer vacancies for yearlings. However, if the food and weather conditions are benign in late summer and autumn, more yearlings may be able to acquire a membership in the flocks than in a poor year. In any case, to a certain limit, joining a flock can be a better option than solitary life, even if the flock became slightly larger than the optimal (Sibly 1983, Pulliam & Caraco 1984, Ekman 1989).

Overall, the proportion of aggressive interactions between Willow Tit flock members is quite low (Ekman & Askenmo 1984, Hogstad 1987a, Lahti et al. 1996), perhaps indicating that the dominance relations are already formed and that the rank of an individual is recognised by others. There is individual variation in the aggressiveness. Especially the top-ranking (alpha) individuals may protect a newly found food patch aggressively from the other flock members. Moreover, males behave more aggressively toward other males than toward females and are less aggressive to their mates than to other birds (Lahti et al. 1996). This may be a reflection of mate protection (e.g. Ekman 1990, Hogstad 1992; see also Section 5.2.).

2.2. Determinants of dominance

Linear hierarchies are common in passerine bird groups (Schneider 1984, Hogstad 1989a, Matthysen 1990), but not a rule without exceptions (Jackson & Winnegrad 1988). The majority of Willow Tit flocks (64 of 68, 94%) studied in northern Finland exhibited a linear social hierarchy (Koivula & Orell 1988, Lahti et al. 1994, 1996, K. Lahti & K. Koivula, unpubl.). Adult male Willow Tits are dominated only by other adult males (Lahti et al. 1996). Yearling males usually rank between adult males and adult females, while yearling females nearly always are at the bottom of the hierarchy. Hogstad (1987a) found a similar dominance hierarchy in the Willow Tit using both feeders and observations of free-foraging birds in Norway, as did also Ekman (1990) in Sweden. In the Finnish population, less than 1% of the interactions between flock members were reversals, i.e. temporary shifts in the dominance order (Lahti et al. 1996). This is in the same magnitude as in a Norwegian population (3%, Hogstad 1987a; see also Ekman 1990, Cristol 1995). The ranks of mates are correlated, so that high-ranking birds were paired with high-ranking birds and low-ranking birds with other low-ranking individuals (Smith 1976, Hogstad 1987a, Lahti et al. 1996).

Numerous factors have been found to correlate with rank in birds: (1) Large size (Watt 1986, Hogstad 1987a), (2) heavy body mass (Røskaft 1983, Hogstad 1987a) and (3) dark or bright — as opposed to light or dull — plumage coloration (Rohwer 1975, Møller 1987) may predict dominance. (4) Males are typically dominant over females (Smith 1976, Arcese & Smith 1985, Enoksson 1988, Koivula & Orell 1988, Nilsson & Smith 1988, Piper & Wiley 1989, Henderson & Hart 1995; but see e.g. Belthoff & Gauthreaux 1991), and (5) older individuals often dominate younger conspecifics of the same sex (Arcese & Smith 1985, Enoksson 1988, Piper & Wiley 1989, Henderson & Hart 1995, Lahti et al. 1996; but see Dhindsa et al. 1989). (6) Site-related dominance has also been described in many species, residents being dominant over intruders (De Laet 1984, Desrochers & Hannon 1989, Piper & Wiley 1989, Lahti et al. 1996). Last, (7) prior residence has often been suggested as a major determinant of dominance (Kikkawa 1980, Hogstad 1987a, Nilsson & Smith 1988, Senar et al. 1990, Wilson 1992).

Support for the effects of many variables on dominance has been given by experimental work: size (Baker & Fox 1978, Jackson 1991, Koivula et al. 1993), coloration (Järvi & Bakken 1984, Jackson 1991, Hogstad & Kroglund 1993; but see Watt 1986, Wilson 1992, Belthoff et al. 1994), sex (Jackson 1991, Bryant & Newton 1996), age (Komers 1989, Cristol et al. 1990, Bryant & Newton 1996; but see Koivula et al. 1993), prior residence (Krebs 1982, Nilsson 1989a, Cristol et al. 1990, Holberton et al. 1990, Koivula et al. 1993), hunger (Popp 1987, Cristol 1992), familiarity with dominant birds, or the 'coat-tail effect' (Wiley 1990), prior winning (Popp 1988), testosterone (Archawaranon et al. 1991), and access to females (Teather & Weatherhead 1995). In experiments, one can exclude the effect of many confounding variables and establish the importance of single factors. However, in natural conditions the dominance relationships are most likely formed as the result of several factors, some of which are intercorrelated (e.g. age and experience), and some of which weigh more than others in a given context.

When controlling for sex and age, size — as measured by tarsus and wing length — does not correlate with rank in the Willow Tit (Lahti et al. 1996). In a Norwegian population, high rank was found to be associated with heavy weight and long wing (Hogstad 1987a). A laboratory study by Koivula et al. (1993) showed size to be an important determinant of dominance in Willow Tit dyads only if the contestants matched in other respects (sex, age and residence). However, prior residence was a strong predictor of dominance, and could at least partly overrule the effect of size and age (Koivula et al. 1993). Although adult Willow Tits are superior to yearlings of the same sex in the field (Ekman & Askenmo 1984, Hogstad 1987a, Koivula & Orell 1988, Ekman 1990, Lahti et al. 1996), this is probably the result of their prior residence (Willow Tits are site tenacious) and not of e.g. adults' greater resource holding potential (Maynard Smith & Parker 1976). The same has been proposed as the cause of adult dominance over first-year birds in Marsh Tits (*Parus palustris*; Nilsson & Smith 1988) and Dark-eyed Juncos (*Junco hyemalis*; Holberton et al. 1990). Therefore, I suggest that it is crucial for a Willow Tit to breed early, so the offspring can reach independence at an early date and the parents are also better able to moult before winter. This may apply also to other species with linear hierarchies in winter flocks. Prior residence improves the probability of acquiring a place and a high ranking position in a winter flock (see also Garnett 1981, Nilsson & Smith 1988, Nilsson 1989a, b, Hogstad 1990a). Early birds to leave the natal area probably find winter flock vacancies in better-quality territories, and also have more time for food hoarding and gaining experience (Ekman 1979a). However, if a Willow Tit breeds late, the offspring should preferably be big and strong, with a large throat badge (Hogstad & Kroglund 1993), so that there might be some possibilities of getting a permanent place in a flock, if the priority is lost. When the place in the flock is established, a Willow Tit should stay in the group, since staying may yield a higher position in the future (Lahti et al. 1996). Naturally, poor conditions such as prolonged cold spells during early spring may select against the propensity to breed early.

2.3. Consequences of dominance

As mentioned earlier, social dominance is often defined as priority to access resources, usually clumped food (e.g. Drews 1993). Dominants may also have prior access to preferred, high-quality food (Langen & Rabenold 1994) or sites with a higher food return (Slotow & Paxinos 1997). However, high rank may become evident in other ways, too. Dominants are able to forage in preferred, safer microhabitats (Schneider 1984, Ekman 1987, Lens & Dhondt 1992) by excluding the subordinates from these parts (Ekman & Askenmo 1984, Hogstad 1988b, Koivula et al. 1994). In times of high predation risk, the dominants can wait before resuming feeding longer than the subordinates (De Laet 1985, Hegner 1985, Hogstad 1988b), most likely since the dominants are in a better physiological condition (Koivula et al. 1995b). Dominants may also possess higher-quality territories and mate earlier in the spring than subordinates (Sherry & Holmes 1989).

All individuals may benefit from flocking (Bertram 1978). However, the benefits may be greater for some than for others. Dominants clearly gain more from living in groups than subordinates in many aspects. They devote less time for scanning, which in turn leaves more time for foraging (Ekman 1987, Waite 1987). High-ranking individuals may kleptoparasitize low-ranking birds (Rohwer & Ewald 1981). They may obtain more food when in a flock compared with when alone, while the subordinates may gain no such advantage of flocking (Baker et al. 1981; but see Slotow & Rothstein 1995). The subordinates may suffer from stress, as indicated by higher levels of plasma corticosterone (Belthoff et al. 1994). The only costs of dominance known to me are: (1) increased fighting (Rohwer & Ewald 1981), and perhaps due to this, (2) a higher metabolic rate (which is energetically expensive) of top-ranking birds, as the result of their dominance status (Røskaft et al. 1986, Hogstad 1987b, Bryant & Newton 1994; but see Reinertsen & Hogstad 1994, Cristol 1995).

The most crucial difference between subordinates and dominants is significantly better winter survival for the socially superior individuals. This phenomenon has been described in a variety of bird genera, especially well in *Parus* (Fretwell 1969, Baker & Fox 1978, Kikkawa 1980, Ekman et al. 1981, Smith 1984, 1994, Arcese & Smith 1985, Hogstad 1988c, 1989b, Koivula & Orell 1988, Ekman 1990, Koivula et al. 1996, Lahti et al. 1998b; but see Bryant & Newton 1996). Most of the data are only correlative and cannot distinguish between dominance status and factors that cause the differences in status. In such a case, the same reasons which cause an individual to rank low (e.g. sickness or some inherent characteristic) may cause also its death. Ekman et al. (1981; Sweden) and Hogstad (1989b; Norway) approached experimentally the question of why dominants survive the winter better. In autumn, Ekman et al. (1981) removed Willow Tit flocks which were soon replaced by immigrants. All replacement tits checked for age were yearlings. The survival in this almost purely yearling population was similar to a control population consisting of adults and yearlings. Because of this, Ekman et al. (1981) suggested that separation from adults might improve yearling survival. In contrast, Hogstad (1989b) removed adults and found the opposite: yearlings survived worse alone than did controls with adults in the flock. The difference was explained by the presence of heterospecific flock members in the Swedish study area, so that the remaining birds could scan less as the result of other species in the flock (Hogstad 1989a). Clearly, more experimental work is needed to reveal the causal relations behind the disappearance of subordinates. According to Koivula et al. (1996), social status affects individual fitness of Willow Tits through rank-dependent survival only, since position in hierarchy as such was not connected to timing or success of breeding.

3. Social dominance and food hoarding

3.1. Effects of time of day, sex, age, and rank

The time of day has been found to affect the probability of storing (Vander Wall 1990). In some bird species, caching is more likely to occur in the morning than in the afternoon (e.g. Powlesland 1980, Lahti & Rytkönen 1996). If the stores made in the morning were used later in the afternoon (Powlesland 1980, Cowie et al. 1981, Stephens & Krebs 1986), this pattern may reflect a routine to postpone the daily build-up of body mass and to maintain high manoeuvrability during the day, thus decreasing predation risk (Lima 1986, Witter & Cuthill 1993, Metcalfe & Ure 1995) still not jeopardising over-night survival (McNamara et al. 1990). Unfortunately, there are no data available on the routines of dominant and subordinate individuals. According to theoretical investigations, dominants could be expected to postpone their daily build-up of internal reserves later in the afternoon than subordinates to reduce predation risk related to increased mass (e.g. Cuthill & Houston 1997). Therefore, differences in daily hoarding–retrieving routine could be expected among the dominance classes: dominants might extend their caching for a longer period during the day.

Individual variation in the caching behaviour may be great (Vander Wall 1990, Lahti & Rytkönen 1996). In the Willow Tit, both sexes store at a similar rate, but yearlings are more likely to hoard than adults (Lahti & Rytkönen 1996). The dominant adults have priority of access to food and safe microhabitats (Ekman & Askenmo 1984, Hogstad 1987a, Koivula et al. 1994). Therefore, the subordinates may use hoarding as a strategy to ensure sufficient reserves (see also Grubb & Pravosudov 1994), perhaps retrieving the food in the afternoon when the dominants are not present, due to flocks dividing into age-specific subgroups during this time of day (Grubb 1987, Hogstad 1988b, own observations). Subordinates may be forced to carry more fat to hedge against starvation (Ekman & Lilliendahl 1993; but see Koivula et al. 1995a), which might explain their tendency to store more, provided they also retrieve more. Hurly (1992) demonstrated that Marsh Tits increase external hoards but not internal fat reserves under highly variable food supply (but see Pravosudov & Grubb 1997). Subordinate Willow Tits might similarly use hoarding — especially short-term hoarding — as a strategy to dampen the fluctuations in their energy intake (cf. Ekman & Hake 1990, Brodin & Clark 1997), compared with dominants which have a more continuous access to food. On the other hand, as the dominants' metabolic rate is higher during the day than that of the subordinates (Hogstad 1987b), low-ranking birds may not need eat as much as the dominants to acquire and to maintain larger reserves. Thus, optimal daily hoarding and foraging routines clearly differ between dominants and subordinates. Whereas dominants can perhaps cache in a more relaxed manner with more certain food access, subordinates are stressed and cache more intensively to ensure sufficient energy intake for survival. However, in time-limited conditions, such as short winter days at high latitudes, birds in different dominance classes may not be able to use different strategies but have to use the whole available time for foraging-related activities (see Section 4).

Top-ranking individuals may cache into the inner parts of branches more than lower-ranking birds (Lahti et al. 1998a). The dominants may have used their priority of access to hoard in the predator-safe inner parts (Ekman 1986, 1987) which also give better protection against bad weather (Lens 1996, Wachob 1996) and snow cover. At variance to Lahti et al. (1998a), the age classes of Willow Tits showed no differences in the use of inner or outer parts of pines in Hogstad (1988b). Weather may explain at least some of this difference between the studies, because Lahti et al. (1998a) conducted their study in warmer weather than Hogstad (1988b), and because Hogstad found that Willow Tits preferred inner parts only in cold weather.

There are contradictory results on the vertical segregation in the cache site selection between the dominance or age classes of the Willow Tit. In discrepancy with previous results (Ekman & Askenmo 1984, Hogstad 1988b, Brodin 1994), Lahti et al. (1998a) found no differences in the vertical caching locations between the dominance classes. Neither did they find differences in the vertical hoarding niche breadths (cf. Woodrey 1991). Again, temperature may have played a role: Hogstad (1988b) described that adults forage in the upper part more than yearlings in cold but not in warm weather. So, the lacking vertical segregation in Finnish Willow Tits could be at least partly a result of lower competition pressure during high temperature conditions. In other words, the adults evict yearlings from inner parts of trees only in energetically more demanding cold weather (cf. Hogstad 1988b). The ephemeral feeder, although resembling natural rich food patches like animal carcasses (Glase 1973), may have affected the caching behaviour. It is possible that when confronting a rich patch, the birds first store the food into temporary sites, in case the ephemeral source disappears. Rehoarding (Brodin 1992) — using memory to recover own stores (Sherry 1989) — might be used later to transport the caches into more segregated niches. Subordinates might also hide clumped food from dominant flock members by scatter hoarding, as suggested by Cowie et al. (1981).

3.2. Social influences on caching behaviour

In free-roaming Willow Tits, the presence of conspecifics seems to suppress the probability of hoarding (Lahti & Rytkönen 1996). Carrascal and Moreno (1993) described a similar pattern in European Nuthatches (*Sitta europaea*) using feeders: when solitary, the birds stored more than when others were present. Black-capped Chickadees (*Parus atricapillus*) made fewer caches in the presence of several conspecifics than when alone or with one conspecific (Stone & Baker 1989). Corvids may even stop hoarding altogether in the presence of others (Källander & Smith 1990, Vander Wall 1990). Subordinates could be expected to be more cautious during caching than dominants, since dominants may rob the food from subordinates. In the Willow Tit, caching distances from feeder were greater when others were nearby compared with when others were absent (Lahti et al. 1998a). The same was found in a small sample of Gray Jays (*Perisoreus canadensis*; Waite 1992).

Dominant Willow Tits cache closer to the feeder than do subordinates (Lahti et al. 1998a). This pattern has been found also in White-breasted Nuthatches (*Sitta carolinensis*; Woodrey 1990) and in interspecific comparisons between dominant nuthatches and subordinate Paridae (Moreno et al. 1981, Petit et al. 1989). Therefore, individuals of low status have to use more energy than high-ranking birds by flying longer distances (Carlson & Moreno 1992) while storing. As shown by Brodin (1993), increasing distance from a feeder may improve the survival of stores, which might partly compensate for the increased flight costs of subordinates compared with dominants. The removal of dominants resulted in a decrease in the hoarding distance, which indicates that the dominants caused the subordinates to carry the caches further from the feeder (Lahti et al. 1998a). This was to my knowledge the first manipulative work to show that it is the presence of dominants that forces the subordinates to space their stores in a wider area. These experimental results imply that the birds may perceive others as a potential source of cache loss and therefore avoid hoarding in their presence. Anecdotal observations in Lahti and Rytkönen (1996) and Lahti et al. (1998a) suggest that especially dominant individuals (both con- and heterospecific) pose a threat to a caching Willow Tit by sometimes pilfering a fresh store or directly robbing the food using their privileged status.

4. Social dominance and the duration of daily activities

4.1. Duration of roosting

Although some attempts have been made to describe the length of activity periods in the non-breeding season (e.g. Franz 1943, Haftorn 1994), there are very few studies which address the effect of dominance on the activity times. Among these, Summers and Feare (1995) found that dominant Starlings (*Sturnus vulgaris*) departed the communal roost earlier than subordinates, contrary to the predictions by the authors. They explained this unexpected result so that dominants leave the roost first and attain the best feeding sites. Overall, the study of activity times is still largely on a descriptive level (but see Lima 1988, Lahti et al. 1997).

Dominant Willow Tits terminate their daily activities earlier and emerge from roost later than subordinate birds (Lahti et al. 1997). This results in a longer duration of roosting for the dominants. Dawn and dusk are conceivably dangerous for diurnal passerines such as Willow Tits. Both diurnal and nocturnal predators may be active at these times (Mikkola 1983), and the vision of tits is probably poorly adapted to crepuscular conditions (Martin 1994). Probably the most serious diurnal predator of wintering Willow Tits in the study area of Lahti et al. (1997), the Pygmy Owl (*Glaucidium passerinum*), shows activity peaks in dawn and dusk. It also preys at least in the breeding season upon Willow Tits more than expected by their abundance (Kellomäki 1977, Mikkola 1983; see also Ekman et al. 1981). Therefore, the longer activity period of the subordinates — falling into the period of dim light — most likely is highly dangerous in terms of predation risk. Indeed, a significant association was found between a long activity period and disappearance (Lahti et al. 1997). This may be an additional mechanism explaining the poor survival rate of subordinates compared with dominants so often found (see Section 2.3.). The subordinates could also have suffered from starvation. They may be worse than dominants in gathering the required amount of energy for over-night survival (Piper & Wiley 1990, Koivula et al. 1995a, Verhulst & Hogstad 1996) and therefore had to extend their day. Furthermore, sometimes subordinates carry more fat than dominants (Ekman & Lilliendahl 1993, Witter & Swaddle 1995, Gosler 1996, Hake 1996). (Actually, any relationship between social dominance and fat storage is possible, depending on the ecological context; Cuthill & Houston 1997.) This can also be risky, especially in the evening, due to increased wing-loading and thus reduced manoeuvrability (Metcalfe & Ure 1995; see also McNamara & Houston 1990, Witter & Cuthill 1993, Houston et al. 1997). To sum up, the beginning and end of daily foraging time need more attention than before and must not be overlooked when accumulating knowledge on e.g. survival or daily fattening strategies.

4.2. The role of internal reserves

The result of the feeding experiment in Lahti et al. (1997) suggested that the level of internal reserves affects the length of active time, as the fed birds shortened their daily active time compared with controls. Similarly, Lima (1988) demonstrated that the activity time of Dark-eyed Juncos was limited by food availability, since birds deprived of food initiated feeding earlier in the morning than controls. Hungry Willow Tits take more risk than satiated ones, whether dominant or subordinate (Koivula et al. 1995b), indicating that the level of internal reserves affects the risk-taking of birds. So, diurnal birds seem to avoid risky times, if they can.

5. Social dominance and survival

5.1. Time-dependence in survival

Lack (1954) proposed that food availability limits the population size of birds. Hence, late winter with short days and depleted non-renewing food resources would be the most difficult time. Slagsvold (1975) suggested that early spring temperature, and territorial behaviour at that time, are critical in the population dynamics of Blue and Great Tits. The idea that late winter (or early spring) is difficult for birds has been fixed in ornithological literature, although without direct evidence. Some studies, however, provide circumstantial support for the idea (e.g. von Haartman 1973).

The mortality rate of Willow Tits in northern Finland is either quite constant from autumn to the following breeding season or peaks in early winter (Lahti et al. 1998b). Since the natal dispersal and irruptive autumn movements are over at that time there (Heikkinen & Tynjälä 1984, own observations; see also Haftorn 1997), dispersal hardly accounts for these peaks. Some of the variation may be explained by colder weather than normally at that time of the year, but probably also other factors, such as predation or food resources, contribute to the observed pattern (Lahti et al. 1998b). The survival probability of Willow Tits exhibited no clear deviations from an even rate in late winter or early spring, unlike in the Black-capped Chickadee (e.g. Smith 1967, Desrochers et al. 1988, Egan & Brittingham 1994), or in yearling Willow Tits in a Swedish population (Ekman 1984). In the Finnish Willow Tit population, the flock territories are large (20–27 ha; Koivula & Orell 1988, Lahti et al. 1996), usually allowing all the surviving flock members to breed within the territory. This may also be a major reason for the low spring dispersal rate observed in that area (Lahti et al. 1998b). Therefore, it seems that there is no need for the adults to evict the surplus yearlings from the breeding grounds [as in Black-capped Chickadees (Smith 1994)], which would result in a spring peak in the yearling disappearance rate (Lahti et al. 1998b). In contrast, Black-capped Chickadees, especially yearlings, seem to be less sedentary in spring (Smith 1967, Weise & Meyer 1979, Desrochers et al. 1988).

This may be at least partly a consequence of much greater densities than in the Willow Tit.

Adult survival can be quite constant throughout the year (Lahti et al. 1998b). Yearlings suffer from greater mortality in winter than in summer, even when the dangerous first months of their lives are excluded. Thus, winter may not be very important in regulating the population size of adult Willow Tits. It is the subordinate yearlings that bear the brunt of the harsh winter.

5.2. Age- and sex-dependence in survival

Yearling Willow Tits are more likely to die in winter than adults (Ekman & Askenmo 1984, Koivula & Orell 1988, Koivula et al. 1996). The survival probability of first-year birds also fluctuates more than that of adults (Lahti et al. 1998b). In addition to age-related experience, adult dominance over yearlings (Hogstad 1987a, Lahti et al. 1996), with priority of access to food and safe sites (Ekman & Askenmo 1984, Hogstad 1988d), may explain this age- (or rank-) dependent survival (Arcese & Smith 1985, Koivula et al. 1996; see Section 2.3.). Secured food supply of dominants minimises starvation risk and enables them to control their level of internal reserves. Subordinates, with more uncertain energy intake, face a greater risk of starvation. Hunger can further expose subordinates to predation: when a bird forages more, it has less time to scan for enemies. Variable access to food may also force subordinates to carry more fat at the expense of reduced manoeuvrability and increased risk of being predated upon (e.g. Cuthill & Houston 1997).

Male and female Willow Tits survive the winter about as likely, although males are dominant over females (Koivula & Orell 1988, Orell et al. 1994, Lahti et al. 1998b). Hogstad (1988d, 1992, 1995) and Ekman (1990) have suggested mate protection as a cause for this discrepancy. The alpha male protects his mate (alpha female) from aggression by other flock members which rank higher than the mate, directs fewer aggressions towards her than towards others (Lahti et al. 1996), allows her to feed in safe microhabitats, and warns her of predators, thereby improving her survival prospects. Thus, the dominant male also has access to a high-quality mate in the following breeding season (Ekman 1990, Hogstad 1992, 1995; see also Lens & Dhondt 1992, 1993 for Crested Tits).

5.3. The importance of food

Food availability restricts Willow Tit winter survival: supplemental food improves the survival significantly (Jansson et al. 1981, Hogstad 1988c, Lahti et al. 1998b). Lack's (1954) winter food limitation hypothesis has been supported by many other studies, too (e.g. Krebs 1971, Smith et al. 1980, Brittingham & Temple 1988, Desrochers et al. 1988, Verhulst 1992, Egan & Brittingham 1994; but see e.g. Krebs 1971, Yom-Tov 1974, Källander 1981, Schmidt & Wolff 1985).

Supplemental food may affect survival directly or indirectly. The most obvious direct effect is reduced starvation. Among the indirect effects is a decreased need to search for food and thus reduced time exposed to predation and increased time for predator surveillance (Jansson et al. 1981). Birds wintering in harsh conditions may benefit more from extra food than birds in more benign environments (Orell 1989). This may be inferred from the fact that none of the studies where food supplementation did not improve survival were conducted in areas with extreme winters, and many negative results have been obtained in non-hoarding Blue and Great Tits (Krebs 1971, Källander 1981, Schmidt & Wolff 1985, Vander Wall 1990). Food hoarding may also play a role; compared with non-hoarders, hoarding individuals possibly have more external reserves left in late winter when non-renewable natural food supply is low. So, the hoarders may not need to leave the territory in search of food, which may cost the territory or the life of the leaving bird. Although food caches without doubt are significant for survival in caching species (Vander Wall 1990), there are, to my knowledge, no detailed studies relating survival and individual differences in hoarding behaviour. In a small data set, Willow Tit individuals that survived until the next breeding season ($N = 9$) did not hoard in September at a greater rate than those that disappeared ($N = 11$) (0.37 vs. 0.35 items cached per minute, respectively, t-test, $t = -0.256$, $df = 18$, $P = 0.80$; see Brodin et al. 1996 for methodology). Manipulative work are needed to explore the importance of caching on survival.

6. Subordinance and flocking

Why do yearlings with a low dominance position stay in flocks, although they obviously pay a greater price than the dominants from life in the group? Subordinates are excluded from food and the safest microhabitats (Ekman & Askenmo 1984, Hogstad 1987a, Koivula et al. 1994). They also have to avoid kleptoparasitizing dominants while hoarding (Lahti et al. 1998a) and take more risk during the day (Hogstad 1988b, Koivula et al. 1994), and extend their activity time into dangerous times at dawn and dusk (Lahti et al. 1997). By the end of winter, subordinates have suffered from a greater mortality rate than dominants (Koivula & Orell 1988, Ekman 1990, Lahti et al. 1998b).

Although flocking is advantageous, flock size cannot grow infinitely (e.g. Sibly 1983, Ekman 1989). All individuals still alive in autumn do not fit in the Willow Tit winter flocks, as can be implied from the presence of non-territorial yearling floaters and their willingness to join a flock (Ekman et al. 1981, Hogstad 1989c, 1990b; floaters are birds without membership in any flock, they use large areas overlapping several flock territories; see Smith 1984). However, there are only a few floaters in northern Finland (Koivula & Orell 1988, Lahti et al. 1996). Perhaps these non-territorial yearlings leave and participate in the large-scale autumnal movements (or die) earlier than in more southern regions. Resident yearling males seem to play a crucial role in the regulation of flock size in the Willow Tit, since they are the ones that most actively evict floaters from the flock (Hogstad 1989c). Ekman (1984) suggested that the flock is composed of as many individuals as the territory can support through the winter. In autumn and early winter there is plenty of food which could temporally feed more birds than there actually are in the flock. As the winter proceeds, the non-renewing food resources diminish. A too large flock could deplete the food reserves totally, so that no birds could survive. However, mortality may lessen the competitive pressure among the remaining flock members in winter, taking also into account that there are no newcomers trying to establish in the flocks anymore.

The decision whether to join a flock appears to be a trade-off between the costs and benefits of group life compared with solitary life. A group offers improved protection from predation and perhaps a more even rate of finding food than living alone. Although other individuals may pose a threat to a foraging or hoarding bird, food searching and storing in a group can be more relaxed than solitary life, e.g. in terms of time used scanning (Carrascal & Moreno 1993). Learning from experienced flock members may also be beneficial (Mönkkönen & Koivula 1993). However, subordinates are stressed in flocks (Silverin et al. 1984) and survive worse than dominants. In comparison to being a group member, a solitary bird needs not spend energy on aggression and may forage in the microhabitats it chooses. On the other hand, living alone forces it to allocate more time to vigilance, and also other benefits of group life are lost. Clearly, costs and benefits constantly affect the decision to flock, since in less risky conditions, for example in warm weather, flock sizes diminish (Hogstad 1988b, Lens & Dhondt 1993). Even if it is costly for a subordinate Willow Tit to submit to the despotic behaviour of dominants, it is a better option to stay in the flock than to adopt a floater strategy: floating yearlings very likely die during the winter (Ekman et al. 1981, Hogstad 1990b), and any possible vacancies in flocks are filled from the bottom rank [Hogstad 1989c; the Willow Tit differs from the Black-capped Chickadee where high-ranking birds that disappear are rapidly replaced by a floater of the same sex, not by the flock's next highest member (Smith 1984)]. Typically, only flock members breed in the following spring (Ekman 1988, Hogstad 1989c). The trade-off between staying or not joining can be viewed as a lack of alternatives, combined with a chance to inherit the territory after the current despot dies ('hopeful dominants'; Ekman 1988, Koivula 1994, Lahti et al. 1996). The floaters may not have chosen the strategy to be outsiders, but they make the best of a bad job (Hogstad 1990b). Selection favours genes that promote flocking behaviour but also genes that affect the behaviour of flock size regulation. As practically all breeders have spent the winter in flocks (assuming also that the tendency to flock is genetically determined), their offspring most likely possess the propensity for this behaviour. As the breeders also most likely have ranked high in the hierarchy, they have probably prevented flock size from growing with aggressive behaviour. The offspring of these successful overwintering individuals then may also have this aptitude.

7. Concluding remarks

Contrary to intuition, winter is not an extremely terrible time for small birds at high latitudes: survival rates may be similar in winter and in summer. The birds are in many ways adapted to the harsh and unpredictable environment. Food availability can be postponed from rich to lean periods by hoarding, and the level of internal reserves is actively regulated to hedge against varying conditions. In addition, flocking promotes predator detection and enhances food finding. The availability of food is a constraint, since extra food improves overwinter survival. This is probably the result of increased protection from predation, and not so much the result of decreased starvation risk, of birds in good condition; they have more time to devote to surveillance and are able to avoid risky times. Subordinates have to take more risks to ensure sufficient reserves for survival, while dominants can use their privilege to access the contested resource, be it food or safety.

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Selostus: **Sosiaalinen eriarvoisuus ja elossasäilyvyys varpuslintuparvissa: hömötiaispainotteinen katsausartikkeli**

Monet linnut viettävät pesimäkausien välisen ajan parvissa, joiden yksilöiden kesken vallitsee selkeä arvojärjestys. Tässä katsauksessa tarkastelen tällaisissa parvissa elävien varpuslintujen elossasäilyvyyttä. Teen selkoa säilyvyyden ja sosiaalisen arvoaseman välisestä yhteydestä ja käyttäytymispiirteistä, jotka saattaisivat selittää havaittuja eroja elossasäilymistodennäköisyydessä. Painopiste on tiaisissa ja erityisesti hömötiaisessa, joiden talvesta selviytymistä on tutkittu runsaasti. Sosiaalinen dominanssi käsitetään suhteelliseksi eikä niinkään yksilön pysyväksi ominaisuudeksi. Dominantti määritellään yleensä sellaiseksi yksilöksi, joka jatkuvasti pääsee ennen toista (eli alisteista) yksilöä käyttämään rajallisia voimavaroja kuten ruokaa tai suojaisia paikkoja. Useilla varpuslintulajeilla korkealle sosiaalisessa hierarkiassa sijoittuvat yksilöt selviytyvät talvesta todennäköisemmin kuin matalalle sijoittuvat. Osan alisteisten suuremmasta kuolleisuudesta selittävät dominantteja epäennustettavampi ravinnonsaanti ja pedoilta turvattomammat paikat. Muita mahdollisia selittäjiä ovat erot ravinnonvarastoinnissa ja aktiivisuusajoissa. Ravinnonvarastointi on monille paikkalinnuille talvesta selviytymisen edellytys. Sosiaalisesti alempiarvoiset linnut voivat käyttää varastointia päivittäisessä ravinnonhankinnassaan eri tavalla kuin korkeampiarvoiset. Alisteiset varastoivat päivän aikana ruokaa — osittain myös piiloon dominanteilta — ja käyttävät näitä kätköjä kerätäkseen pitkäksi talviyöksi tarvittavan varaenergian. Asemansa ansiosta dominanttien ravinnonsaanti on turvatumpaa kuin alisteisilla, eikä niillä ole niin suurta painetta käyttää varastointia lyhytaikaisena puskurina kuin alisteisilla. Ainakin joillakin lajeilla osa varastoista syödään vasta viikkojen tai kuukausien kuluttua. Dominantit pysyttelevät suojassa alisteisia pidempään pedon hyökkäyksen jälkeen. Dominantit myös aloittavat talvipäivinä aktiivisuutensa myöhemmin ja vetäytyvät yöpuulle aikaisemmin kuin alisteiset. Tämä on tulkittu petoriskin pienentämiseksi, koska esim. varpuspöllö saalistaa mieluimmin juuri aamu- ja iltahämärissä, ja koska päiväaktiiviset varpuslinnut eivät mitä ilmeisimmin näe kovin hyvin hämärässä. Alisteisten täytyy työskennellä pidempään ja ottaa päivälläkin suurempia riskejä todennäköisesti sen vuoksi, että ne ovat dominantteja heikommassa kunnossa. Parveutumisesta on sekä hyötyä (esim. parantunut petosuoja) että haittaa (useampia kuluttamassa ravintovaroja), mutta hyöty voi olla dominanteille suurempi kuin alisteisille. Siitä huolimatta parveen liittyminen useimmiten kannattaa: alisteisena parvessa talvesta selviytyy todennäköisemmin kuin yksin.

References

Andersson, M. & Krebs, J. 1978: On the evolution of hoarding behaviour. — Anim. Behav. 26: 707–711.

Arcese, P. & Smith, J. N. M. 1985: Phenotypic correlates and ecological consequences of dominance in Song Sparrows. — J. Anim. Ecol. 54: 817–830.

Archawaranon, M., Dove, L. & Wiley, R. H. 1991: Social inertia and hormonal control of aggression and dominance in White-throated Sparrows. — Behaviour 118: 42–65.

Baker, M. C. & Fox, S. F. 1978: Dominance, survival, and enzyme polymorphism in Dark-eyed Juncos, Junco hyemalis. — Evolution 32: 697–711.

Baker, M. C., Belcher, C. S., Deutsch, L. C., Sherman, G. L. & Thompson, D. B. 1981: Foraging success in Junco flocks and the effects of social hierarchy. — Anim. Behav. 29: 137–142.

Bednekoff, P. A. & Balda, R. P. 1996: Social caching and observational spatial memory in Pinyon Jays. — Behaviour 133: 807–826.

Belthoff, J. R. & Gauthreaux, S. A., Jr. 1991: Aggression and dominance in House Finches. — Condor 93: 1010–1013.

Belthoff, J. R., Dufty, A. M., Jr. & Gauthreaux, S. A., Jr. 1994: Plumage variation, plasma steroids and social dominance in male house finches. — Condor 96: 614–625.

Bernstein, I. S. 1981: Dominance: the baby and the bathwater. — Behav. Brain Sci. 4: 419–457.

Bertram, B. R. C. 1978: Living in groups: predators and prey. — In: Krebs, J. R. & Davies, N. B. (eds.), Behavioural ecology: an evolutionary approach: 64–96. Blackwell Scientific Publications, Oxford.

Biebach, H. 1996: Energetics of winter and migratory fattening. — In: Carey, C. (ed.), Avian energetics and nutritional ecology: 280–323. Chapman & Hall, New York.

Blem, C. R. 1990: Avian energy storage. — Curr. Orn. 7: 59–113.

Brittingham, M. C. & Temple, S. A. 1988: Impacts of supplemental feeding on survival rates of Black-capped Chickadees. — Ecology 69: 581–589.

Brodin, A. 1992: Cache dispersion affects retrieval time in hoarding Willow Tits. — Ornis Scand. 23: 7–12.

Brodin, A. 1993: Low rate of loss of Willow Tit caches may increase adaptiveness of long-term hoarding. — Auk 110: 642–646.

Brodin, A. 1994: Separation of caches between individual Willow Tits hoarding under natural conditions. — Anim. Behav. 47: 1031–1035.

Brodin, A. & Clark, C. W. 1997: Long-term hoarding in the Paridae: a dynamic model. — Behav. Ecol. 8: 178–185.

Bryant, D. M. & Newton, A. V. 1994: Metabolic costs of dominance in Dippers, Cinclus cinclus. — Anim. Behav. 48: 447–455.

Bryant, D. M. & Newton, A. V. 1996: Dominance and survival of Dippers Cinclus cinclus. — Behav. Ecol. Sociobiol. 38: 173–181.

Carlson, A. & Moreno, J. 1992: Cost of short flights in the Willow Tit measured with doubly-labeled water. — Auk 109: 389–393.

Carrascal, L. M. & Moreno, E. 1993: Food caching versus immediate consumption in the Nuthatch: the effect of social context. — Ardea 81: 135–141.

Cowie, R. J., Krebs, J. R. & Sherry, D. F. 1981: Food storing by Marsh Tits. — Anim. Behav. 29: 1252–1259.

Cristol, D. A. 1992: Food deprivation influences dominance status in Dark-eyed Juncos, Junco hyemalis. — Anim. Behav. 43: 117–124.

Cristol, D. A. 1995: Costs of switching social groups for dominant and subordinate Dark-eyed Juncos (Junco hyemalis). — Behav. Ecol. Sociobiol. 37: 93–101.

Cristol, D. A., Nolan, V., Jr. & Ketterson, E. D. 1990: Effect of prior residence on dominance status of Dark-eyed Juncos, Junco hyemalis. — Anim. Behav. 40: 580–586.

Cuthill, I. C. & Houston, A. I. 1997: Managing time and energy. — In: Krebs, J. R. & Davies, N. B. (eds.), Behavioural ecology: an evolutionary approach. 4 ed: 97–120. Blackwell Science, Cambridge.

Dawkins, R. 1982: The extended phenotype. — Oxford Univ. Press, Oxford.

De Laet, J. F. 1984: Site-related dominance in the Great Tit Parus major major. — Ornis Scand. 15: 73–78.

De Laet, J. F. 1985: Dominance and anti-predator behaviour of Great Tits Parus major: a field study. — Ibis 127: 372–377.

Desrochers, A. & Hannon, S. J. 1989: Site-related dominance and spacing among winter flocks of Black-capped Chickadees. — Condor 91: 317–323.

Desrochers, A., Hannon, S. J. & Nordin, K. E. 1988: Winter survival and territory acquisition in a northern population of Black-capped Chickadees. — Auk 105: 727–736.

Dewsbury, D. A. 1982: Dominance rank, copulatory behavior, and differential reproduction. — Q. Rev. Biol. 57: 135–159.

Dhindsa, M. S., Komers, P. E. & Boag, D. A. 1989: The effect of familiarity with an environment on the dominance relationships between juvenile and adult Black-billed Magpies. — Ornis Scand. 20: 187–192.

Drews, C. 1993: The concept and definition of dominance in animal behaviour. — Behaviour 125: 283–313.

Egan, E. S. & Brittingham, M. C. 1994: Winter survival rates of a southern population of Black-capped Chickadees. — Wilson Bull. 106: 514–521.

Ekman, J. 1979a: 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. 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. — Anim. Behav. 35: 445–452.

Ekman, J. 1988: Subordination costs and group territoriality in wintering Willow Tits. — Acta XIX Congr. Int. Orn. 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 and reproductive success in male–female associations. — Behav. Ecol. Sociobiol. 26: 239–245.

Ekman, J. B. & Askenmo, C. E. H. 1984: Social rank and habitat use in Willow Tit groups. — Anim. Behav. 32: 508–514.

Ekman, J. B. & Hake, M. K. 1990: Monitoring starvation risk: adjustments of body reserves in Greenfinches (Carduelis chloris L.) during periods of unpredictable foraging success. — Behav. Ecol. 1: 62–67.

Ekman, J. B. & Lilliendahl, K. 1993: Using priority to food access: fattening strategies in dominance-structured Willow Tit (Parus montanus) flocks. — Behav. Ecol. 4: 232–238.

Ekman, J., Cederholm, G. & Askenmo, C. 1981: Spacing and survival in winter groups of Willow Tit Parus montanus and Crested Tit P. cristatus — a removal study. — J. Anim. Ecol. 50: 1–9.

Elgar, M. A. 1989: Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. — Biol. Rev. 64: 13–33.

Enoksson, B. 1988: Age- and sex-related differences in dominance and foraging behaviour of Nuthatches Sitta europaea. — Anim. Behav. 36: 231–238.

Franz, J. 1943: Ueber Ernährung und Tagesrhythmus einiger Vögel im arktischen Winter. — J. Orn. 91: 154–165.

Fretwell, S. 1969: Dominance behavior and winter habitat distribution in Juncos (Junco hyemalis). — Bird-Banding 40: 1–25.

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

Glase, J. C. 1973: Ecology of the social organization in the Black-capped Chickadee. — Living Bird 12: 235–267.

Gosler, A. G. 1996: Environmental and social determinants of winter fat storage in the Great Tit Parus major. — J. Anim. Ecol. 65: 1–17.

Grubb, T. C., Jr. 1987: Changes in the flocking behaviour of wintering English titmice with time, weather and supplementary food. — Anim. Behav. 35: 794–806.

Grubb, T. C., Jr. & Pravosudov, V. V. 1994: Towards a general theory of energy management in wintering birds. — J. Avian Biol. 25: 255–260.

Haftorn, S. 1956: Contribution to the food biology of tits especially about storing of surplus food. Part IV. A comparative analysis of Parus atricapillus L., P. cristatus L., and P. ater L. — Kgl. Norske Vidensk. Selsk. Skr. 1956(4): 1–54.

Haftorn, S. 1990: Social organization of winter flocks of Willow Tits Parus montanus in a Norwegian subalpine birch forest. — In: Blondel, J., Gosler, A., Lebreton, J.-D. & McCleery, R. (eds.), Population biology of passerine birds — an integrated approach. NATO ASI Series, Series G 24: 401–413. Springer-Verlag, Berlin.

Haftorn, S. 1994: Diurnal rhythm of passerines during the polar night in Pasvik, North Norway, with comparative notes from South Norway. — Fauna norv. Ser. C, Cinclus 17: 1–8.

Haftorn, S. 1997: Natal dispersal and winter flock formation in the Willow Tit Parus montanus. — Fauna norv. Ser. C, Cinclus 20: 17–35.

Hake, M. 1996: Fattening strategies in dominance-structured Greenfinch (Carduelis chloris) flocks in winter. — Behav. Ecol. Sociobiol. 39: 71–76.

Hand, J. L. 1986: Resolution of social conflicts: dominance, egalitarianism, spheres of dominance, and game theory. — Q. Rev. Biol. 61: 201–220.

Hegner, R. E. 1985: Dominance and anti-predator behaviour in Blue Tits (Parus caeruleus). — Anim. Behav. 33: 762–768.

Heikkinen, J. & Tynjälä, M. 1984: Lintujen syysmuutto Pohjois-Pohjanmaalla 1983. — Aureola 9: 71–80.

Henderson, I. G. & Hart, P. J. B. 1995: Dominance, food acquisition and reproductive success in a monogamous passerine: the Jackdaw Corvus monedula. — J. Avian Biol. 26: 217–224.

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. — Auk 104: 333–336.

Hogstad, O. 1988a: Advantages of social foraging of Willow Tits Parus montanus. — Ibis 130: 275–283.

Hogstad, O. 1988b: Rank-related resource access in winter flocks of Willow Tits Parus montanus. — Ornis Scand. 19: 169–174.

Hogstad, O. 1988d: Social rank and antipredator behaviour of Willow Tits Parus montanus in winter flocks. — Ibis 130: 45–56.

Hogstad, O. 1988c: The influence of energy stress on social organization and behaviour of Willow Tits Parus montanus. — Fauna norv. Ser. C, Cinclus 11: 89–94.

Hogstad, O. 1989a: Social organization and dominance behavior in some Parus species. — Wilson Bull. 101: 254–262.

Hogstad, O. 1989b: Subordination in mixed-age bird flocks - a removal study. — Ibis 131: 128–134.

Hogstad, O. 1989c: The role of juvenile Willow Tits, Parus montanus, in the regulation of winter flock size: an experimental study. — Anim. Behav. 38: 920–925.

Hogstad, O. 1990a: Dispersal date and settlement of juvenile Willow Tits Parus montanus in winter flocks. — Fauna norv. Ser. C, Cinclus 13: 49–55.

Hogstad, O. 1990b: Winter floaters in Willow Tits Parus montanus: a matter of choice or making the best of a bad situation. — In: Blondel, J., Gosler, A., Lebreton, J.-D. & McCleery, R. (eds.), Population biology of passerine birds - an integrated approach. NATO ASI Series, Series G 24: 415–421. Springer-Verlag, Berlin.

Hogstad, O. 1992: Mate protection in alpha pairs of wintering Willow Tits, Parus montanus. — Anim. Behav. 43: 323–328.

Hogstad, O. 1995: Alarm calling by Willow Tits, Parus montanus, as mate investment. — Anim. Behav. 49: 221–225.

Hogstad, O. & Kroglund, R. T. 1993: The throat badge as a status signal in juvenile male Willow Tits Parus montanus. — J. Orn. 134: 413–423.

Holberton, R. L., Hanaho, R. & Able, K. P. 1990: Age-related dominance in male Dark-eyed Juncos: effect of plumage and prior residence. — Anim. Behav. 40: 573–579.

Houston, A. I., Welton, N. J. & McNamara, J. M. 1997: Acquisition and maintenance costs in the long-term regulation of avian fat reserves. — Oikos 78: 331–340.

Huntingford, F. A. & Turner, A. K. 1987: Animal conflict. — Chapman & Hall, London.

Hurly, T. A. 1992: Energetic reserves of Marsh Tits (Parus palustris): food and fat storage in response to variable food supply. — Behav. Ecol. 3: 181–188.

Jackson, W. M. 1991: Why do winners keep winning? — Behav. Ecol. Sociobiol. 28: 271–276.

Jackson, W. M. & Winnegrad, R. L. 1988: Linearity in dominance hierarchies: a second look at the individual attributes model. — Anim. Behav. 36: 1237–1240.

Jansson, C., Ekman, J. & von Brömssen, A. 1981: Winter mortality and food supply in tits Parus spp. — Oikos 37: 313–322.

Järvi, T. & Bakken, M. 1984: The function of the variation in the breast stripe of the Great Tit (Parus major). — Anim. Behav. 32: 590–596.

Källander, H. 1981: The effects of provision of food in winter on a population of the Great Tit Parus major and the Blue Tits P. caeruleus. — Ornis Scand. 12: 244–248.

Källander, H. & Smith, H. G. 1990: Food storing in birds: an evolutionary perspective. — Curr. Orn. 7: 147–207.

Kaufman, J. F. 1983: On the definitions and functions of dominance and territoriality. — Biol. Rev. 58: 1–20.

Kellomäki. E. 1977: Food of the Pygmy Owl Glaucidium passerinum in the breeding season. — Ornis Fennica 54: 1–29.

Kikkawa, J. 1980: Winter survival in relation to dominance classes among Silvereyes Zosterops lateralis chlorocephala of Heron Island, Great Barrier Reef. — Ibis 122: 437–446.

Koivula, K. 1994: Social dominance in Willow Tit (Parus montanus) flocks: causes and effects on resource access, survival, and reproduction. — Acta Univ. Oul. A 263: 1–36.

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. & Rytkönen, S. 1993: Prior residency as a key determinant of social dominance in the Willow Tit (Parus montanus). — Behav. Ecol. Sociobiol. 33: 283–287.

Koivula, K., Lahti, K., Rytkönen, S. & Orell, M. 1994: Do subordinates expose themselves to predation? Field experiments on feeding site selection by Willow Tits. — J. Avian Biol. 25: 178–183.

Koivula, K., Orell, M., Rytkönen, S. & Lahti, K. 1995a: Fatness, sex and dominance; seasonal and daily body mass changes in Willow Tits. — J. Avian Biol. 26: 209–216.

Koivula, K., Rytkönen, S. & Orell, M. 1995b: Hunger-dependency of hiding behaviour after a predator attack in dominant and subordinate Willow Tits. — Ardea 83: 397–404.

Koivula, K., Orell, M. & Rytkönen, S. 1996: Winter survival and breeding success of dominant and subordinate Willow Tits Parus montanus. — Ibis 138: 624–629.

Komers, P. E. 1989: Dominance relationships between juvenile and adult Black-billed Magpies. — Anim. Behav. 37: 256–265.

Krebs, J. R. 1971: Territory and breeding density in the Great Tit, Parus major L. — Ecology 52: 2–22.

Krebs, J. R. 1982: Territorial defence in the Great Tit (Parus major): do residents always win? — Behav. Ecol. Sociobiol. 11: 185–194.

Krebs, J. R. & Davies, N. B. (eds.) 1991: Behavioural ecology: an evolutionary approach. 3 ed. — Blackwell Scientific Publications, Oxford.

Lack, D. 1954: The natural regulation of animal numbers. — Clarendon Press, Oxford.

Lahti, K. & Rytkönen, S. 1996: Presence of conspecifics, time of day and age affect Willow Tit food hoarding. — Anim. Behav. 52: 631–636.

Lahti, K., Koivula, K. & Orell, M. 1994: Is the social hierarchy always linear in tits? — J. Avian Biol. 25: 347–348.

Lahti, K., Koivula, K., Orell, M. & Rytkönen, S. 1996: Social dominance in free-living Willow Tits Parus montanus: determinants and some implications of hierarchy. — Ibis 138: 539–544.

Lahti, K., Koivula, K. & Orell, M. 1997: Dominance, daily activity and winter survival in Willow Tits: detrimental cost of long working hours? — Behaviour 134: 921–939.

Lahti, K., Koivula, K., Rytkönen, S., Mustonen, T., Welling, P., Pravosudov, V. V. & Orell, M. 1998a: Social influences on food caching in Willow Tits: a field experiment. — Behav. Ecol. 9. (In press.)

Lahti, K., Orell, M., Rytkönen, S. & Koivula, K. 1998b: Time and food-dependence in Willow Tit winter survival. — Ecology 79. (In press.)

Langen, T. A. & Rabenold, K. N. 1994: Dominance and diet selection in Juncos. — Behav. Ecol. 5: 334–338.

Lens, L. 1996: Wind stress affects foraging site competition between Crested Tits and Willow Tits. — J. Avian Biol. 27: 41–46.

Lens, L. & Dhondt, A. A. 1992: Variation in coherence of Crested Tit winter flocks: an example of multivariate optimization. — Acta Œcologica 13: 553–567.

Lens, L. & Dhondt, A. A. 1993: Individual variation in mate care by alpha males in Crested Tit winter flocks. — Behav. Ecol. Sociobiol. 33: 79–85.

Levin, S. A., Cohen, D. & Hastings, A. 1984: Dispersal strategies in patchy environments. — Theor. Popul. Biol. 26: 165–191.

Lima, S. L. 1986: Predation risk and unpredictable feeding conditions: determinants of body mass in birds. — Ecology 67: 377–385.

Lima, S. L. 1988: Initiation and termination of daily feeding in Dark-eyed Juncos: influences of predation risk and energy reserves. — Oikos 53: 3–11.

Ludescher, F.-B. 1973: Sumpfmeise (Parus p. palustris L.) und Weidenmeise (P. montanus salicarius Br.) als sympatrische Zwillingsarten. — J. Orn. 114: 3–56.

Martin, G. R. 1994: Form and function in the optical structure of birds eyes. — In: Davies, M. N. O. & Green, P. R. (eds.), Perception and motor control in birds: an ecological approach: 5–34. Springer-Verlag, Berlin.

Matthysen, E. 1990: Nonbreeding social organization in Parus. — Curr. Orn. 7: 209–249.

Maynard Smith, J. & Parker, G. A. 1976: The logic of asymmetric contests. — Anim. Behav. 24: 159–175.

McNamara, J. M. & Houston, A. I. 1990: The value of fat reserves and the tradeoff between starvation and predation. — Acta. Biotheor. 38: 37–61.

McNamara, J. M., Houston, A. I. & Krebs, J. R. 1990: Why hoard? The economics of food hoarding in tits, Parus spp. — Behav. Ecol. 1: 12–23.

Metcalfe, N. B. & Ure, S. E. 1995: Diurnal variation in flight performance and hence potential predation risk in small birds. — Proc. R. Soc. Lond. B 261: 395–400.

Mikkola, H. 1983: Owls of Europe. — T. & A. D. Poyser, Calton.

Møller, A. P. 1987: Variation in badge size in male House Sparrows Passer domesticus: evidence for status signalling. — Anim. Behav. 35: 1637–1644.

Mönkkönen, M. & Koivula, K. 1993: Neophobia and social learning of foraging skills in Willow Tits Parus montanus. — Ardea 81: 43–46.

Moreno, J., Lundberg, A. & Carlson, A. 1981: Hoarding of individual Nuthatches Sitta europaea and Marsh Tits Parus palustris. — Holarct. Ecol. 4: 263–269.

Nilsson, J.-Å. 1989a: Establishment of juvenile Marsh Tits in winter flocks: an experimental study. — Anim. Behav. 38: 586–595.

Nilsson, J.-Å. 1989b: Causes and consequences of natal dispersal in the Marsh Tit, Parus palustris. — J. Anim. Ecol. 58: 619–636.

Nilsson, J.-Å. & Smith, H. G. 1988: Effects of dispersal date on winter flock establishment and social dominance in Marsh Tits Parus palustris. — J. Anim. Ecol. 57: 917–928.

Orell, M. 1989: Population fluctuations and survival of Great Tits Parus major dependent on food supplied by man in winter. — Ibis 131: 112–127.

Orell, M., Rytkönen, S. & Koivula, K. 1994: Causes of divorce in the monogamous Willow Tit, Parus montanus, and consequences for reproductive success. — Anim. Behav. 48: 1143–1154.

Petit, D. R., Petit, L. J. & Petit, K. E. 1989: Winter caching ecology of deciduous woodland birds and adaptations for protection of stored food. — Condor 91: 766–776.

Piper, W. H. & Wiley, R. H. 1989: Correlates of dominance in wintering White-throated Sparrows: age, sex and location. — Anim. Behav. 37: 298–310.

Piper, W. H. & Wiley, R. H. 1990: The relationship between social dominance, subcutaneous fat, and annual survival in wintering White-throated Sparrows (Zonotrichia albicollis). — Behav. Ecol. Sociobiol. 26: 201–208.

Popp, J. W. 1987: Resource value and dominance among American Goldfinches. — Bird Behav. 7: 73–77.

Popp, J. W. 1988: Effects of experience on agonistic behaviour among American Goldfinches. — Behav. Proc. 16: 11–19.

Powlesland, R. G. 1980: Food-storing behaviour of the South Island Robin. — Mauri Ora 8: 11–20.

Pravosudov, V. V. & Grubb, T. C., Jr. 1997: Management of fat reserves and food caches in tufted titmice (Parus bicolor) in relation to unpredictable food supply. — Behav. Ecol. 8: 332–339.

Pulliam, H. R. & Caraco, T. 1984: Living in groups: is there an optimal group size. — In: Krebs, J. R. & Davies, N. B. (eds.), Behavioural ecology: an evolutionary approach. 2 ed.: 122–147 Blackwell Scientific Publications, Oxford.

Reinertsen, R. E. 1996: Physiological and ecological aspects of hypothermia. — In: Carey, C. (ed.), Avian energetics and nutritional ecology: 125–157. Chapman & Hall, New York.

Reinertsen, R. E. & Hogstad, O. 1994: Influence of social status on the nocturnal energy expenditure of the Willow Tit Parus montanus. — Fauna norv. Ser. C, Cinclus 17: 43–48.

Roberts, G. 1996: Why individual vigilance declines as group size increases. — Anim. Behav. 51: 1077–1086.

Rohwer, S. 1975: The social significance of avian winter plumage variability. — Evolution 29: 593–610.

Rohwer, S. & Ewald, P. W. 1981: The cost of dominance and advantage of subordination in a badge signaling system. — Evolution 35: 441–454.

Røskaft, E. 1983: The relationship between the fledging weights of captive rooks and position in the dominance hierarchy one year later. — Fauna norv. Ser. C, Cinclus 6: 78–80.

Røskaft, E., Järvi, T., Bakken, M., Bech, C. & Reinertsen, R. E. 1986: The relationship between social status and resting metabolic rate in Great Tits (Parus major) and Pied Flycatchers (Ficedula hypoleuca). — Anim. Behav. 34: 838–842.

Schmidt, K.-H. & Wolff, S. 1985: Hat die Winterfütterung einen Einfluss auf Gewicht und Überlebensrate von

Kohlmeisen (Parus major)? — J. Orn. 126: 175–180.

Schneider, K. J. 1984: Dominance, predation, and optimal foraging in White-throated Sparrow flocks. — Ecology 65: 1820–1827.

Senar, J. C., Copete, J. L. & Metcalfe, N. B. 1990: Dominance relationships between resident and transient wintering siskins. — Ornis Scand. 21: 129–132.

Sherry, D. F. 1989: Food storing in the Paridae. — Wilson Bull. 101: 289–304.

Sherry, T. W. & Holmes, R. T. 1989: Age-specific social dominance affects habitat use by breeding American Redstarts (Setophaga ruticilla): a removal experiment. — Behav. Ecol. Sociobiol. 25: 327–333.

Sibly, R. M. 1983: Optimal group size is unstable. — Anim. Behav. 31: 947–948.

Silverin, B., Viebke, P.-A. & Westin, J. 1984: Plasma levels of luteinizing hormone and steroid hormones in free-living winter groups of Willow Tits (Parus montanus). — Horm. Behav. 18: 367–379.

Slagsvold, T. 1975: Critical period for regulation of Great Tit (Parus major L.) and Blue Tit (Parus caeruleus L.) populations. — Norw. J. Zool. 23: 67–88.

Slotow, R. & Paxinos, E. 1997: Intraspecific competition influences food return — predation risk trade-off by White-crowned Sparrows. — Condor 99: 642–650.

Slotow, R. & Rothstein, S. I. 1995: Influence of social status, distance from cover, and group size on feeding and vigilance in White-crowned Sparrows. — Auk 112: 1024–1031.

Smith, D. C. & Van Buskirk, J. 1988: Winter territoriality and flock cohesion in the Black-capped Chickadee Parus atricapillus. — Anim. Behav. 36: 466–476.

Smith, J. N. M., Montgomerie, R. D., Taitt, M. J. & Yom-Tov, Y. 1980: A winter feeding experiment on an island Song Sparrow population. — Oecologia (Berl.) 47: 164–170.

Smith, S. M. 1967: Seasonal changes in the survival of the Black-capped Chickadee. — Condor 69: 344–359.

Smith, S. M. 1976: Ecological aspects of dominance hierarchies in Black-capped Chickadees. — Auk 93: 95–107.

Smith, S. M. 1984: Flock switching in chickadees: why be a winter floater. — Am. Nat. 123: 81–98.

Smith, S. M. 1994: Social influences on the dynamics of a northeastern Black-capped Chickadee population. — Ecology 75: 2043–2051.

Stephens, T. A. & Krebs, J. R. 1986: Retrieval of stored seeds by Marsh Tits Parus palustris in the field. — Ibis 128: 513–525.

Stone, E. & Baker, M. C. 1989: The effects of conspecifics on food caching by Black-capped Chickadees. — Condor 91: 886–890.

Summers, R. W. & Feare, C. J. 1995: Roost departure by European Starlings Sturnus vulgaris: effects of competition and choice of feeding site. — J. Avian Biol. 26: 289–295.

Teather, K. L. & Weatherhead, P. J. 1995: The influence of age and access to females on dominance in captive male Brown-headed Cowbirds (Molothrus ater). — Can. J. Zool. 73: 1012–1018.

Vander Wall, S. B. 1990: Food hoarding in animals. — Univ. of Chicago Press, Chicago.

Verhulst, S. 1992: Effects of density, beech crop and winter feeding on survival of juvenile Great Tits; an analysis of Kluyver's removal experiment. — Ardea 80: 285–292.

Verhulst, S. & Hogstad, O. 1996: Social dominance and energy reserves in flocks of Willow Tits. — J. Avian Biol. 27: 203–208.

von Haartman, L. 1973: Talgmespopulationen på Lemsjöholm. — Lintumies 8: 7–9.

Wachob, D. G. 1996: The effect of thermal microclimate on foraging site selection by wintering Mountain Chickadees. — Condor 98: 114–122.

Waite, T. A. 1987: Vigilance in the White-breasted Nuthatch: effects of dominance and sociality. — Auk 104: 429–434.

Waite, T. A. 1992: Social hoarding and a load size–distance relationship in Gray Jays. — Condor 94: 995–998.

Watt, D. J. 1986: Relationship of plumage variability, size and sex to social dominance in Harris' Sparrows. — Anim. Behav. 34: 16–27.

Weise, C. M. & Meyer, J. R. 1979: Juvenile dispersal and development of site-fidelity in the Black-capped Chickadee. — Auk 96: 40–55.

Wiley, R. H. 1990: Prior-residence and coat-tail effects in dominance relationships of male Dark-eyed Juncos, Junco hyemalis. — Anim. Behav. 40: 587–596.

Wilson, E. O. 1975: Sociobiology: the new synthesis. — Belknap Press, Cambridge.

Wilson, J. D. 1992: A re-assessment of the significance of status signalling in populations of wild Great Tits, Parus major. — Anim. Behav. 43: 999–1009.

Witter, M. S. & Cuthill, I. C. 1993: The ecological costs of avian fat storage. — Phil. Trans. R. Soc. Lond. B 340: 73–92.

Witter, M. S. & Swaddle, J. P. 1995: Dominance, competition, and energetic reserves in the European Starling, Sturnus vulgaris. — Behav. Ecol. 6: 343–348.

Woodrey, M. S. 1990: Economics of caching versus immediate consumption by White-breasted Nuthatches: the effect of handling time. — Condor 92: 621–624.

Woodrey, M. S. 1991: Caching behavior in free-ranging White-breasted Nuthatches: the effects of social dominance. — Ornis Scand. 22: 160–166.

Yom-Tov, Y. 1974: The effect of food and predation on breeding density and success, clutch size and laying date of the Crow (Corvus corone L.). — J. Anim. Ecol. 43: 479–498.