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SOCIAL ORGANIZATION AND DOMINANCE BEHAVIOR IN SOME *PARUS* SPECIES

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ABSTRACT.—Several *Parus* species live in small, coherent, winter flocks with a dominance hierarchy in which males usually dominate females and adults dominate juveniles. By allocating time to aggression, dominant adults secure the best resources, such as feeding sites and cover against predator, while subordinate juveniles are prevented from using preferred microhabitats. Juveniles, therefore, have higher predation risks than adults. Accordingly, winter survival of adults is higher than that of juveniles. Social dominance entails an increased metabolic rate during the daylight period, but not during night. Subordinates presumably accept their submissive roles while waiting for a chance to improve their social rank positions by replacing dead, high-ranking adults.

Parids remaining at higher latitudes throughout the year are confronted by low ambient temperature, snow cover, periods of food shortage, and short days. Air temperature affects the birds directly, by increasing energy demand, and small birds have relatively high energy requirements (Calder 1974, Calder and King 1974, Kendeigh et al. 1977). Therefore, during cold winter days, parids spend most of the day foraging (Gibb 1954, Ulfstrand 1962, Hogstad 1988a). The winter survival of tits is clearly affected by the severity of the winter (e.g., Ticehurst and Hartley 1948, Kluijver 1951, Gibb 1960) but seems modified by the food supply (Gibb 1960, Perrins 1965, von Haartman 1973). Improved survival of Great Tits (*Parus major*) (von Haartman 1973), Willow Tits (*P. montanus*) (Jansson et al. 1981, Hogstad 1988d) and Crested Tits (*P. cristatus*) (Jansson et al. 1981) when provided with extra food reveals that food availability is crucial to survival. Nighttime is probably the most difficult period for survival. The short period of daylight in mid-winter restricts the available foraging time and necessitates a nocturnal fasting period of up to 18–19 h. Although several species use protected roosting-sites, such as dense foliage, or holes in snow or trees (Kendeigh 1961, Sulkava 1969, Andreev 1980, Korhonen 1981), or utilize nocturnal hypothermia to limit their energy expenditure (Reinertsen and Haftorn 1983), they have to maintain a high rate of energy intake during the few available hours of daylight. However, foraging time may be restricted because of vigilance for predators. To enhance feeding efficiency and reduce the individual risks of predation, tits may congregate in flocks. Individuals in flocks often are able to detect an approaching predator sooner than solitary individuals

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(Pulliam 1973, Powell 1974, Bertram 1978, Lazarus 1979), and each member of the flock can therefore allocate more time to other activities such as foraging (Caraco 1979, Caraco et al. 1980, Studd et al. 1983).

Energy stress and predation are probably main factors responsible for winter mortality of parids. Since juveniles seem to suffer more from cold and predation than do adults (e.g., Ekman et al. 1981, Ekman 1984, Hogstad 1988d), it might be suggested that this difference in winter mortality is determined more by social interactions than by environmental factors. The present paper gives some examples of the effect of social factors on the behavior of parids living in stable winter flocks.

Social organization.—All *Parus* species live in social units in winter, either in temporary aggregations or in stable flocks, the "nucleus" of which often consists of a former breeding pair. Species known to live in such stable flocks are Black-capped (*P. atricapillus*), Carolina (*P. carolinensis*), and Mountain chickadees (*P. gambeli*), Tufted Titmice (*P. bicolor*), and Crested, Willow, and Marsh tits (*P. palustris*). Such flocks form during late summer and early autumn as juvenile tits, after family breakup and a dispersal period, become sedentary and join a mated pair. These social flocks usually contain a small number of non-kin members that defend their territory against flocks of conspecifics during autumn and winter (Löhrl 1950, Dixon 1965, Glase 1973, Smith 1976, Ekman 1979a, Weise and Meyer 1979, Brawn and Samson 1983, Hogstad 1987a, Rost 1987, Nilsson 1988, T. C. Grubb Jr., pers. comm.).

Within such conspecific flocks a linear dominance hierarchy is established in which males dominate females and adults dominate juveniles (Glase 1973, Smith 1976, Ficken et al. 1981, Hogstad 1987a). The hierarchical order is established during flock formation in late summer and autumn, and, unless some members disappear, the hierarchy remains stable throughout the winter. Factors affecting dominance are age, sex, seniority in the flock, body size, and plumage coloration (Glase 1973, Saitou 1979, Brawn and Samson 1983, Järvi and Bakken 1984, Nilsson and Smith 1985, Hogstad 1987a, Nilsson 1988).

The number of conspecifics per flock varies, but usually consists of one adult mated pair and 2–4 juveniles (Glase 1973, Ekman 1979a, Hogstad 1987a, Rost 1987). The juveniles also probably establish pairbonds, in which females have dominance ranks parallel to that of their mates (Dixon 1963, Smith 1984, Hogstad 1987a). In the Great Tit, however, the juveniles do not seem to establish pairbonds as long as they are associated with adults in stable winter flocks (Saitou 1978). Since adult and juvenile Willow Tits chase their mates less frequently than other female flock members, and since females are less vigilant when accompanied by their mates, mate protection is suggested (Hogstad 1988c, d).

Flock size seems dependent on the absence or presence of congeneric species in the area (Hogstad 1988b). Because vigilance level, aggression, and intraspecific competition usually increase with flock size (Fretwell 1972, Caraco 1979), fewer birds of more than one species can form mixed-species flocks. The number of individuals that form single-species flocks is often larger than the number of conspecific individuals in mixed-species flocks (Buskirk 1976, Hogstad 1988b). This may be explained as optimization between predator evasion and reduction of food competition (e.g., Alatalo et al. 1986). Thus, the individual vigilance time in Willow Tits was found to be affected more by the total flock size of Willow Tits and Coal Tits (*P. ater*) than by the number of Willow Tits alone (Hogstad 1988b). Most parids, therefore, participate in mixed-species winter flocks, and the individuals benefit from the presence of the other species (cf. Krebs 1973, Morse 1977, Sullivan 1984, Pöysä 1985).

Although flocks of several species consist of permanent members that only occasionally leave their territory, the flocks often split up into subflocks for minutes or as long as several hours. The degree of flock coherence increases with temperature stress and energy requirement, which indicates that energetic considerations are important for flock behavior. Increased flock sizes in cold weather have been observed for Tufted Titmice (Morse 1970), Carolina Chickadees (Morse 1970), Great Tits (Hinde 1952; Morse 1970, 1978; Saitou 1978), Blue Tits (*P. caeruleus*) (Morse 1970, 1978), Marsh Tits (Lüdescher 1973), and Willow Tits (Lüdescher 1973, Hogstad 1984, 1988b, d).

An unknown, but probably substantial proportion of juvenile parids does not succeed in achieving permanent flock membership. The existence of such non-territorial juvenile birds, or floaters, that do not settle as resident flock members in autumn has been observed among Tufted Titmice (Samson and Lewis 1979), Great Tits (Drent 1983), Blue Tits, (Colquhoun 1942), Marsh Tits (Morley 1950, Nilsson and Smith, 1988), Black-capped Chickadees (Smith 1976, 1984, 1987; Samson and Lewis 1979; Weise and Meyer 1979) and Willow and Crested tits (Ekman 1979a, b; Ekman et al. 1981). When such non-territorial Willow Tits visited flocks of conspecifics in a Norwegian subalpine forest during September, they were accepted as members of flocks of four or five, but they were prevented by the resident birds from joining flocks consisting of six members, probably the optimal flock size of Willow Tits in that area (Hogstad, in press). The juvenile resident males were especially aggressive and chased the newcomers away (see also Nilsson 1988 for Marsh Tits). The greater aggression of juveniles compared to that of adults may be explained in terms of fitness. A further increase in flock size would probably affect the fitness of the subdominant juveniles more negatively than that of the dominant adults which have priority of access to contested resources. Since these non-territorial juveniles lower their fitness by staying outside social territorial flocks (cf. Rubenstein 1976, Rubenstein et al. 1977), their chances of surviving the winter seem poor (Ekman 1979a, b; Ekman et al. 1981, Nilsson 1986).

Dominance behavior.—The costs and benefits among flock members differ, and a skewed access in favor of the dominants to resources such as feeding sites and cover against predators has been verified for Blue Tits (de Laet 1985), Black-capped Chickadees (Glase 1973), and Willow Tits (Ekman and Askenmo 1984; Hogstad 1988a, c). Among Willow Tits, the subordinate juveniles are apparently prevented by the adults from using the preferred upper half of coniferous trees, a region that probably provides greater protection from predation than the lower half (Ekman and Askenmo 1984, Ekman 1986, Hogstad 1988c). Tits prefer to feed close to protected cover, and because of their social dominance, higher-ranked Willow Tits use feeding sites close to cover more frequently than lower-ranked flock members. They even prevent subordinates from using such feeding sites (Ekman 1987, Hogstad 1988a). As a consequence, juveniles have to increase their vigilance time (Ekman 1987). Subordinate Willow Tits that foraged in close presence of adults also increased their vigilance time to keep dominants under surveillance so as to reduce the chance of their being attacked or kleptoparasitized (Hogstad 1988a, d). Because they spend time watching dominants in addition to predator vigilance, the energy budget of subordinates is likely more strained than that of adults. The sequence of return of Willow Tits to a feeding site after a life-like, stuffed predator placed close to the site was removed was correlated with dominance rank of Willow Tits, showing that it was the subordinates that took the greatest risks of predation (Hogstad 1988a). The adults apparently behaved more cautiously than the juveniles, and they reduced their potential rate of food intake in order to reduce the risk of predation to a greater degree than the juveniles. By being subject to less stress (Silverin et al. 1984) and probably being in better physiological condition than subordinates, dominants can afford to take less risks (cf. de Laet 1985, Hegner 1985).

In Willow Tits, it is usually the top-ranked bird among the juvenile flock members that replaces dead dominant adults of its own sex (Hogstad 1987b, unpubl. data). A high rank is therefore essential for improving winter survival chances of juveniles.

The dominance asymmetry within flocks obviously forces juveniles to pay for their membership. Despite having fewer benefits than dominant flock members, subordinates benefit from improved predator vigilance by being in a flock, especially during severe weather conditions (Ekman

1987, Hogstad 1988b). When the energy stress is lessened, e.g., in mild weather or when the birds are provided with extra food, the total vigilance level can be maintained even in small flocks (Jansson et al. 1981, Berner and Grubb 1985, Ekman 1987). Under such conditions, it seems more profitable for juvenile Willow Tits to avoid company with dominant adults and to forage in less predator-risky habitats such as in the upper half of conifers (Hogstad 1988d).

However, social dominance also entails an extra energetic cost. The metabolic rate, or oxygen consumption rate of Willow Tits, increases with the social dominance status. The alpha male in a flock may have up to 25% higher oxygen consumption than the lowest-ranking bird in the same flock (Hogstad 1987b). After removal of the alpha male from a flock, the beta male became the top-ranked member of the flock. Concomitantly, his oxygen consumption rate increased significantly more than that of the other members in the flock. After removal of one of the subordinates, only minor changes were recorded in the oxygen consumption of the remaining flock members. Thus, the metabolic rate of a flock member is not stable but is conditional upon its dominance rank (Hogstad 1987b). During nighttime, however, no such relationship between dominance rank and nocturnal metabolic rate was found (Reinertsen and Hogstad, unpubl. data). The oxygen consumption rates of dominant males and subordinate females decreased to the same level during the nighttime period. This strongly indicates that the relation between social rank and metabolic rate is primarily due to the difference in activity linked to social role. Since the alpha male is the most aggressive in defending the flock territory against conspecific flocks (Hogstad 1987a), this activity also is likely to be reflected in its metabolic rate. Although dominant individuals have higher energy requirements during daytime, they gain the best access to the available food resources and therefore probably have no difficulty in compensating for this extra cost. During nighttime, however, both dominants and subordinates depend on the energy reserves built up during the daylight period, a reserve that must last throughout the night because it is impossible to replace until the next day.

Instead of devoting relatively large proportions of their energy budgets to aggressive behavior, subordinates presumably accept their submissive roles and do not fight higher-ranking individuals. This acceptance by subordinates is the intrinsic value of dominance. Subordinates probably make the best of their actual situation while waiting for a higher social status with maturity. Although the majority of the juveniles die during their first winter, some are able to improve their social rank by replacing dominant adults that die during winter. For tits in hierarchical flocks, subordination may therefore be viewed as a conditional strategy.

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