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# It Is Expensive To Be Dominant

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Many animals spend long periods in groups. The advantages of being a group member, compared with solitary living, include improved predator avoidance and increased feeding efficiency (Pulliam and Caraco 1984). However, the costs and benefits involved may differ among the group members. The results of in-dividual contests are usually heavily biased in favor of the dominant individuals, who generally obtain more food, enjoy a more protected position within the group, and enjoy improved chances of survival than do their subordinates (Baker and Fox 1978, Kik-kawa 1980, Morse 1980, Baker et al. 1981). By allo-cating time to aggression, dominant individuals may increase their chances of daily survival (Pulliam and Caraco 1984), even if they risk being hurt. The ben-efits of dominance can be diminished, however, by more frequent involvement in aggressive encounters (Järvi and Bakken 1984). An increase in the metabolic rate, due to more frequent aggressive encounters and mediated through hormone levels, could represent one proximate pathway of meeting the costs of dom-inance (cf. Røskaft et al. 1986). Based on the func-tional relationship that exists between endocrine ac-tivity and metabolism (Silver et al. 1979, Hänssler and Prinzinger 1979), one would predict that a rela-tionship should exist between the metabolic rate and the social status of each group member, and that a change in social status will entail changes in the met-abolic rate, especially among the dominants. I tested these predictions by manipulating the composition of free-ranging, winter flocks of Willow Tits (*Parus montanus*).

The Willow Tit is a highly sedentary European species. Breeding pairs remain in their exclusive areas throughout the year. During the winter these areas are defended by small, non-kin flocks, formed as the roaming yearlings become sedentary and join the adults during the late summer and autumn. Once established, stable hierarchies are maintained in these flocks during the winter.

I studied Willow Tits living in a subalpine mixed forest in central Norway. The social rank order of six members of each of six such winter flocks, and oxy-gen-consumption rates of each bird, were studied. All birds were caught in mist-nets or feeder-traps during August–October 1984. They were individ-ually color-banded, aged, and their wing lengths were measured. The dominant-subordinate relationships within each flock were determined by observation of the outcomes of behavioral interactions at feeders placed in the center of the territory of each of the flocks studied (Hogstad 1987).

The experiments were made between November 1984 and January 1985. Oxygen-consumption rates were measured by using a manometric respirometer (with a 20% KOH solution as $CO_2$ absorber) connect-ed to a compensatory chamber (Dixon 1934). Con-stant pressure was maintained by injecting pure oxy-gen into the respirometer chamber, and the amount of oxygen injected equaled the amount of oxygen consumed. All values are given in STP conditions. The measurements were made between 1100 and 1300 at an ambient temperature of 5°C. The birds were caught 1–12 min before the experiments started, and were kept in the dark during the experiments. The body mass of each bird was recorded before the start of each experiment. Immediately after measuring their oxygen-consumption rates, all birds, except the most dominant one in three flocks and one of the subor-dinates in the three other flocks, were released in their original territories. A week later, the oxygen-consumption rates of the five birds released in each flock, and their present social rank order within the same flocks, were redetermined.

The initial oxygen-consumption rates of the indi-vidual birds varied considerably, ranging from 9.7 to 12.6 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ (Table 1). This variation could be due to differences in body size, age, sex, or domi-nance status. The intercorrelations among these fac-tors are given in Table 2. A multiple regression anal-

TABLE 1. Data recorded for the individual Willow Tits studied, before and after removal of one bird from each flock.

| Flock | Individual | Age (yr) | Wing length (mm) | Social rank order | Before removal | | After removal | |
|---|---|---|---|---|---|---|---|---|
| | | | | | Body mass (g) | Oxygen consumption rate[a] | Body mass (g) | Oxygen consumption rate[a] |
| F1 | Adult male | 3 | 67 | 6 | 13.0 | 11.4 | — | — |
| | Juvenile male | 1 | 67 | 5 | 12.2 | 10.8 | 12.4 | 11.4 |
| | Juvenile male | 1 | 67 | 4 | 12.0 | 10.7 | 12.2 | 11.0 |
| | Adult female | 3 | 64 | 3 | 12.0 | 11.0 | 11.6 | 10.8 |
| | Juvenile female | 1 | 63 | 2 | 11.4 | 10.2 | 11.2 | 10.0 |
| | Juvenile female | 1 | 63 | 1 | 11.2 | 9.7 | 11.2 | 9.8 |
| F2 | Adult male | 2 | 68 | 6 | 13.0 | 11.8 | — | — |
| | Juvenile male | 1 | 67 | 5 | 12.6 | 10.9 | 12.8 | 11.7 |
| | Juvenile male | 1 | 67 | 4 | 12.6 | 10.8 | 12.6 | 10.9 |
| | Adult female | 2 | 66 | 3 | 11.8 | 10.9 | 11.6 | 10.8 |
| | Juvenile female | 1 | 62 | 2 | 11.4 | 10.4 | 11.2 | 10.3 |
| | Juvenile female | 1 | 63 | 1 | 11.4 | 10.3 | 11.4 | 10.1 |
| F3 | Adult male | 2 | 67 | 6 | 12.0 | 11.8 | — | — |
| | Juvenile male | 1 | 67 | 5 | 11.8 | 11.0 | 12.0 | 11.5 |
| | Juvenile male | 1 | 66 | 4 | 11.8 | 10.7 | 11.8 | 10.9 |
| | Adult female | 2 | 64 | 3 | 11.8 | 10.9 | 11.8 | 11.0 |
| | Juvenile female | 1 | 64 | 2 | 11.2 | 11.3 | 11.2 | 11.1 |
| | Juvenile female | 1 | 64 | 1 | 11.4 | 10.2 | 11.4 | 10.2 |
| F4 | Adult male | 4 | 68 | 6 | 12.8 | 12.6 | 12.6 | 12.4 |
| | Juvenile male | 1 | 67 | 5 | 12.0 | 12.0 | 11.8 | 11.9 |
| | Juvenile male | 1 | 67 | 4 | 11.8 | 10.8 | 11.6 | 10.8 |
| | Adult female | 2 | 65 | 3 | 11.8 | 10.6 | — | — |
| | Juvenile female | 1 | 63 | 2 | 11.0 | 9.8 | 11.2 | 9.8 |
| | Juvenile female | 1 | 63 | 1 | 11.0 | 10.2 | 11.0 | 10.0 |
| F5 | Adult male | 2 | 68 | 6 | 12.2 | 11.8 | 12.0 | 11.8 |
| | Juvenile male | 1 | 67 | 5 | 11.6 | 11.1 | 11.6 | 11.3 |
| | Juvenile male | 1 | 67 | 4 | 11.4 | 11.0 | 11.6 | 11.1 |
| | Adult female | 2 | 64 | 3 | 11.4 | 10.5 | 11.2 | 10.4 |
| | Juvenile female | 1 | 64 | 2 | 11.4 | 10.4 | — | — |
| | Juvenile female | 1 | 63 | 1 | 11.0 | 10.0 | 11.2 | 9.8 |
| F6 | Adult male | 2 | 67 | 6 | 13.2 | 12.4 | 13.2 | 12.4 |
| | Juvenile male | 1 | 66 | 5 | 13.2 | 12.2 | 13.0 | 12.0 |
| | Juvenile male | 1 | 65 | 4 | 12.2 | 11.8 | 12.0 | 11.7 |
| | Adult female | 2 | 64 | 3 | 12.0 | 11.6 | 11.8 | 11.3 |
| | Juvenile female | 1 | 62 | 2 | 11.6 | 9.8 | — | — |
| | Juvenile female | 1 | 63 | 1 | 11.8 | 9.8 | 11.8 | 9.8 |

[a] ml $O_2 \cdot g^{-1} \cdot h^{-1}$.

ysis revealed that dominance rank alone accounted for 67% of the overall variation in oxygen-consumption rate, while the remaining factors together accounted for only 5% (not significant). Oxygen-consumption rate also was correlated significantly and positively with social rank for 5 of the 6 flocks studied (Fig. 1). Such a positive correlation between oxygen-consumption rate and dominance rank has been found previously in experiments with flocks of Great Tits (*Parus major*) held in captivity (Røskaft et al. 1986).

When handled, Willow Tits of different dominance rank showed no differences in physical activity. Because a high rank order appears to restrain the acute adrenalin response to the stress induced by capture (Schwabl et al. 1986), neither an increase in activity nor an adrenal response to capture stress can account for the higher oxygen-consumption rate of the dominant Willow Tits.

After removal of the dominant males [the alpha bird; dominance rank (dr) = 6] from three of the flocks (F1–3), the next dominant (beta) male became the dominant member in the flock. Concomitantly, oxygen-consumption rates of the new alpha males increased ($\bar{x} = 0.63 \pm 0.15$ SD ml $O_2 \cdot g^{-1} \cdot h^{-1}$; Fig. 1). This change was significantly greater than in the other four members of the same flocks ($\bar{x} = -0.02 \pm 0.17$ ml $O_2 \cdot g^{-1} \cdot h^{-1}$; $P < 0.01$, Mann-Whitney $U$-test).

After removal of one of the subordinate birds from the other three flocks (viz. the adult female, dr = 3, F3; or the dominant juvenile female, dr = 2, F5–6),
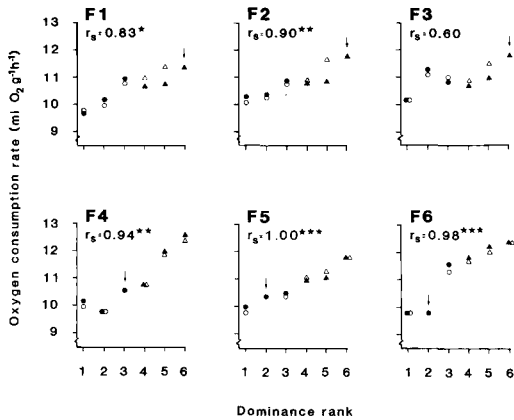
Fig. 1. Oxygen-consumption rates of male (triangles) and female (circles) Willow Tits in 6 winter flocks (F1–6) relative to their respective dominance rankings. Symbols denote the oxygen-consumption rate before (black) and after (white) removal of one individual from each flock (arrow). The most dominant bird is ranked 6. The Spearman rank correlation coefficients (one-tailed), $r_s$, are based on the relationships that existed before removal. * = $P < 0.05$, ** = $P < 0.01$, and *** = $P < 0.001$.

TABLE 2. Intercorrelation matrix for the different characteristics of the Willow Tits studied (based on the values presented in Table 1).

|  | Mass | Age | Sex | Dominance status |
|---|---|---|---|---|
| Wing length (mm) | 0.69 | 0.30 | 0.90 | 0.91 |
| Body mass (g) | — | 0.47 | 0.68 | 0.79 |
| Age |  | — | 0.08 | 0.43 |
| Sex |  |  | — | 0.88 |
| Dominance status |  |  |  | 0.82 |

only insignificant changes were recorded in the oxygen-consumption rates of the remaining four flock members ($\bar{x} = -0.07 \pm 0.13$ ml $O_2 \cdot g^{-1} \cdot h^{-1}$). Hence, a change in the social status of males, but not of females, in Willow Tit flocks resulted in a change in the oxygen-consumption rate.

When the alpha bird of a flock was removed, the second (beta) bird advanced and became the new alpha bird. The mean oxygen-consumption rate of the three new alpha birds (11.5 ml $O_2 \cdot g^{-1} \cdot h^{-1}$) did not differ significantly from that of four original alpha birds in neighboring flocks (11.8 ml $O_2 \cdot g^{-1} \cdot h^{-1}$). Within its own flock, the new alpha individual already dominated all the other members, and an increase in metabolic rate would appear to have been an unnecessary energetic cost for holding the highest-ranking status. Other functions may be linked with the alpha position, however, such as defense of the flock territory against conspecific flocks. The high-ranking Willow Tits are always the most aggressive when two flocks meet close to their common territorial boundary (Hogstad 1987). The alpha bird therefore would be expected to exhibit aggression at approximately the same level as the alpha birds of the other flocks, and this should be reflected in its metabolic rate.

Thus, the metabolic rate of flock members is not stable, but is conditional on their dominance rank. A shift from a lower to a higher dominance rank will involve, for a male, an increase in its metabolic rate. No similar correlation between the rank of the fe-

males and their metabolic rates was found, probably because their rank position, in relation to other flock members of the same sex, follows from the dominance rank of their mates (Hogstad 1987). The oxygen-consumption rates of dominant males and of subordinate females, however, decreased to exactly the same level during the nighttime rest period (Hogstad and Reinertsen unpubl. data), indicating that the relationship found between social status and metabolic rate was due primarily to the difference in activity linked to social role.

Although dominant Willow Tits secure the best habitats (Ekman and Askenmo 1984) and have a better winter survival rate (Ekman 1984), social dominance obviously entails an extra energetic cost. This cost sets an upper limit to the degree of despotism that it is economical for a dominant to exercise. Otherwise it is hard to see why dominants should not increase the energy resources allocated to this activity, so long as they thereby benefit from it. One possible reason is that such a bias in resource allocation might result in the departure of the subordinates from the flock and a breakdown of the entire social system.

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# The "Snapshot" Count for Estimating Densities of Flying Seabirds During Boat Transects: A Cautionary Comment

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Most early surveys of seabirds from shipboard were designed to collect information on distribution and relative abundance (see Tasker et al. 1984). More recently, several investigators have attempted to translate observations at sea into absolute densities and, in some cases, estimate standing crop biomass and energy transfer (Wiens et al. 1978, Schneider and Hunt 1982, Powers 1983, Ainley et al. 1984, Blake et al. 1984). This practice is likely to grow as interest increases in the impacts of seabirds on marine ecosystems.

Most investigators have estimated densities by means of strip transects, usually 300 m wide and lasting from 10 to 30 min. The methodology and biases of strip transects have been investigated extensively for terrestrial situations (Hayne 1949; Anderson and Pospahala 1970; Emlen 1971, 1977; Eberhardt 1978; Burnham and Anderson 1984), but in all of these studies the birds censused were regarded as stationary objects. At sea a high proportion of birds counted are flying, and the majority move faster than the shipborne observer (Gaston et al. 1987). This causes a problem in deriving instantaneous densities because most of the birds seen are in flight and, hence, the chance of their entering the observer's field is a function of their speed relative to the ship.

Some investigators have ignored this potential source of bias (Powers 1983, Ainley et al. 1984), while others have discussed it without correcting for it (Wiens et al. 1978). Recently, Tasker et al. (1984) suggested a technique to eliminate the bias caused by bird movements. They suggested that birds in flight should be counted by means of a series of instantaneous "snapshots." Hence, if the ship covers 2.5 km in the course of a 10-min watch, and if flying birds are visible up to 0.5 km away, then five "snapshot" counts will be made of the area within the transect up to 0.5 km ahead to provide an estimate of the density of flying birds on the transect.

Under ideal conditions the method outlined by Tasker et al. (1984) should yield results unbiased by bird movements. Any snapshot count, however, is bound to involve a finite time period (Haney 1985). To investigate how the time taken to complete the "snapshot" might affect the bias caused by bird movements, we developed a simulation model based on a simplified transect of fixed width. The model is based on formulae 8 and A9 of Gaston and Smith (1984):

$$N = Dt(w|S - s \cos r| + as|\sin r|),$$

where $N$ = number of birds counted within the transect, $D$ = true density of flying birds (birds/km$^2$), $t$ =