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The effect of dominance rank on fat deposition and food hoarding in the Willow Tit *Parus montanus* – an experimental test

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We studied the effects of dominance rank on fat deposition and hoarding behaviour in Willow Tits *Parus montanus*. Dominant individuals can displace subordinates which gives them priority to new food sources; they can also pilfer stored food from subordinates. This gives subordinates less certain access than dominants both to their own caches and to new food sources. Theory predicts that subordinates should invest more than dominants both in body fat reserves and stored food. Empirical evidence is equivocal; some studies have shown that subordinates built up larger reserves than dominants, whereas others show the opposite. In an earlier indoor experiment, Pravosudov and Lucas found no effect of rank on either hoarding rate or fat reserves, but the experimental design was such that the results were ambiguous. This paper reports on a similar, but improved, experiment in outdoor aviaries. However, our results agree with the earlier experiment, since we found no effect of rank on either food storing or fat deposition. The reasons for this are explored.

INTRODUCTION

Body fat and cached food are two manifestations of the same phenomenon: energy reserves must be stored for future use. Organisms need energy stores because energy need is continuous while food intake is intermittent, and food availability varies with short- and long-term fluctuations. However, energy stores are not entirely beneficial because building them up and maintaining them may be costly. Many examples of such costs in birds can be given; predation risk or metabolic rate may be higher for fatter birds, time and energy must be spent in transporting food while caching, and such flights may increase the probability of being spotted by a predator, etc.

The question of how much to invest in energy storing is a typical optimality problem, benefits and costs should be weighed against each other. If costs and/or benefits vary with dominance rank, the optimal investment should differ between individuals of different rank. For example, in food-storing bird species dominant individuals can steal stored food from subordinates more easily than the reverse (Lahti & Rytönen 1996, Brodin *et al.* 2001). This imbalance

between ranks does not depend only on different costs and benefits of energy storing, but may also arise if access to food differs with rank. Building up fat reserves must be easier for dominant individuals since they can displace subordinates from food sources and choose the best microhabitats (Ekman & Askenmo 1984, Hogstad 1987, Brodin 1994b). It seems reasonable that dominance rank should affect hoarding strategies as well as fat acquisition strategies.

In hoarding species, fat acquisition and food storing are different behaviours that will affect each other. For example, if a bird's fat reserves in the evening are too small, it will eat food it encounters even if it also needs to store. Thus we must control for the level of fat reserves in order to understand hoarding decisions. The contrary may also be true, a hoarding bird with large supplies of stored food may decide to carry smaller body fat reserves than a bird without any stored food.

Many species in the family Paridae (tits, titmice and chickadees) live in dominance structured groups and invest heavily in food storing (Ekman 1989). For example, Willow Tits *Parus montanus* store tens of thousands of seeds and larvae each autumn for consumption during the winter, at least in regions with cold winters (Haftorn 1956, 1974, Pravosudov 1985, Brodin 1994a). Fat acquisition strategies have also

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been studied in the Willow Tit (Ekman & Lilliendahl 1993, Clark & Ekman 1995, Koivula *et al.* 1995). Since winter flocks are small it is reasonable to describe the social system in such a species as a simple two-rank system with dominant and subordinate individuals (Brodin *et al.* 2001).

Earlier studies on energy storing in food-hoarding birds disagree on the effect of dominance rank. Ekman and Lilliendahl (1993) found that dominant Willow Tits were leaner than subordinate birds in south-central Sweden. In Northern Finland Koivula *et al.* (1995) found the opposite, subordinates were leaner than dominants. In one field study, Pravosudov (1985) found that dominant Willow Tits and Siberian Tits *P. cinctus* stored more than subordinates. In another field study and a feeder experiment Lahti and Rytkönen (1996) and Lahti (1998) found the opposite, subordinate Willow Tits stored more than dominants. In a theoretical model, Clark and Ekman (1995) predicted that subordinates should carry larger fat reserves than dominants when food is abundant but that both categories should carry the same amount of fat when food is less abundant. In another theoretical model Brodin *et al.* (2001) predicted that subordinates should store more than dominants since they must hedge against pilfering by dominants. In an indoor experiment on Carolina Chickadees *P. carolinensis*, Pravosudov and Lucas (2000) found that neither the amount of fat carried nor the number of seeds stored was affected by rank. In summary, there seem to be three contradictory predictions for how social rank should affect the amount of energy stored as body fat and cached food: (i) subordinates should build up larger reserves than dominants, (ii) dominants should use their priority access to food to build up larger reserves and (iii) rank should have no effect on energy storing.

In experiments on captive birds it is possible to control for factors that may vary in the field. Such experiments may therefore be the best way to investigate phenomena like the effect of rank on energy-storing behaviour. In the experiment above, Pravosudov and Lucas (2000) compared birds when they foraged in a pair to how they acted when they foraged alone. Such a design, however, may make it difficult to detect rank effects for two reasons. First, it is not clear how a solitary bird evaluates its rank. Secondly, there may be differences in foraging behaviour that depend on group effects rather than rank, for example if birds in company assess the situation as more competitive than when foraging by themselves.

Another problem in aviary studies of hoarding behaviour is the large variation in how individual birds behave in captivity. Typically, some individuals will start storing immediately, others will require training in order to store at all and, finally, some individuals will never adapt to the artificial environment (e.g. Brodin & Kunz 1997). Such large individual variation may make it difficult to detect effects that in fact may be quite large.

The purpose of this study was to test the effect of dominance rank on fat acquisition and hoarding behaviour in a similar way to Pravosudov and Lucas (2000). We aimed to improve their design by (i) minimizing the effect of individual differences and (ii) controlling for factors other than rank. The first we achieved by comparing the behaviour of each bird when it foraged together with a bird over which it was dominant to when it foraged with another bird to which it was subordinate. The second we achieved by making all replicates in the same social context, i.e. a pair of birds.

METHODS

Aviaries

We used outdoor aviaries measuring approximately $3.5 \times 3.5 \times 2.5$ m. The floor of the aviaries consisted mainly of moss and sand and the walls were made of non-transparent corrugated plastic. The top of the aviaries was covered with double nets, and the birds could only see the sky, not the surroundings. In each aviary there was an observation booth that was accessible from outside. The booths were equipped with one-way windows, which allowed us to study the birds without disturbing them. There were plenty of places in the aviaries in which sunflower seeds could be cached, e.g. in the ground, in crevices in the walls or in artificial 'hoarding trees' that we had constructed. These consisted of 2-m-high rods with holes drilled in them to allow food to be cached (see Brodin & Kunz 1997 for a more detailed description). We furnished the interior of the aviaries with branches and nestboxes to provide a more natural environment with several refuges and roosting places.

We kept the birds on a diet of non-hoardable food (animal and vegetable matter, ground into powder), and the only hoardable food the birds came in contact with was sunflower seeds that we provided during training sessions and tests. We marked all birds individually with colour rings, and performed the study during the autumns and winters of 1998 and 1999.

Training of birds and experiment

Before each test session we placed two birds in the same aviary for 2 days. This was sufficient for them to get used to the environment and establish a rank order. Before each replicate, we deprived the birds of food for 1 h in order to increase motivation to eat and hoard. We then placed a tray of sunflower seeds in the aviary for 1 h. During this time, we observed and noted how many seeds the birds ate and stored. Competition, mostly in the form of displacement at the food source, happened frequently during the tests. We repeated the test once every second day between 11:00 and 14:00 h with five replicates for each pair of birds. After that, we formed new pairs, matching birds so that the dominant bird became subordinate in the new pair, and the subordinate became dominant in another new pair.

The rank-position of each studied bird was only changed once. Following the change, a 2-day acclimatization period was given, during which the birds could get used to their new rank. A change in rank like this – as a result of predation, migration or other factors that affect flock composition – is not unlikely in nature and the birds should be able to respond and adapt to the new situation.

We weighed the birds to the nearest 0.1 g during the hoarding sessions with an electronic balance (Mettler Toledo) placed inside the aviary. On top of the balance we had mounted a perch that the birds frequently used. To minimize the risk of influences depending on the time of day, we only used weighings taken between 11:00 and 14:00 h. We assume that changes in mass are largely due to changes in fat reserves. We only handled the birds when we needed to move them between aviaries.

We controlled for all factors we thought possibly could confound the results, using the following control procedure: (i) Each individual's behaviour as a subordinate was compared to its own behaviour as a dominant. With this paired design we balanced the effect of individual differences in behaviour. (ii) Many earlier hoarding experiments have been made indoors at room temperature but we used outdoor aviaries with natural temperatures and light regimes. (iii) We weighed the birds repeatedly during each monitoring period to measure changes in body fat reserves. (iv) We performed all experiments around midday to minimize time of day variation in motivation to store. (v) We carried out five repeated monitoring sessions with each pair of birds to minimize effects of temporary and unusual behaviours.

RESULTS

Fat reserves indicated by mass

Of 14 birds that cached regularly during training, we could use nine as both dominants and subordinates. We made five replicates for each dyad of birds. Body mass was higher in three birds when they acted as dominants and lower in the other six birds (Fig. 1). In two birds there was a significant difference of almost 2 g in mass between their two rank roles (Fig. 1, bird 1: 11.9 ± 0.42 (se) g, 10.1 ± 0.07 g and bird 2: 10.1 ± 0.26 g, 12.0 ± 0.40 g). One of these birds was 'leaner' as a subordinate, the other as a dominant. In the other seven the mass stayed relatively constant through the study (Fig. 1). Overall, the mass did not differ when birds changed dominance roles ($P = 0.47$, $n = 9$, paired t -test, two-tailed).

Hoarded reserves

The average number of stored seeds (Fig. 2) was slightly larger for dominants (mean 7.1 ± 2.50) than for subordinates (mean 5.5 ± 1.90) but this difference was not significant ($P > 0.78$, $n = 9$, paired t -test, two-tailed). Five birds stored more as dominants and four as subordinates. In only one bird was the difference significant (Fig. 2, bird 9: 13 ± 5.56 seeds as dominant), but this bird did not store at all when it acted as a subordinate.

The results for both fat acquisition and hoarding were far from being significant in any direction. This made it pointless for us to continue the experiments and increase sample sizes.

DISCUSSION

Our results do not support the prediction that dominance rank should affect energy storing behaviour (Clark & Ekman 1995, Brodin *et al.* 2001). Instead it agreed with the finding of Pravosudov and Lucas (2000) that there is no such effect. Neither for fat acquisition nor for hoarding was there a difference in any direction. Furthermore, our balanced experimental design makes it unlikely that any confounding factor concealed any differences that we possibly could have detected in our experimental set-up. We conclude that there simply was no effect of rank on hoarding or fat storage in our experiment and that there may be three reasons for this.

First, the theoretical predictions that subordinates invest more in energy storing than dominants (Clark

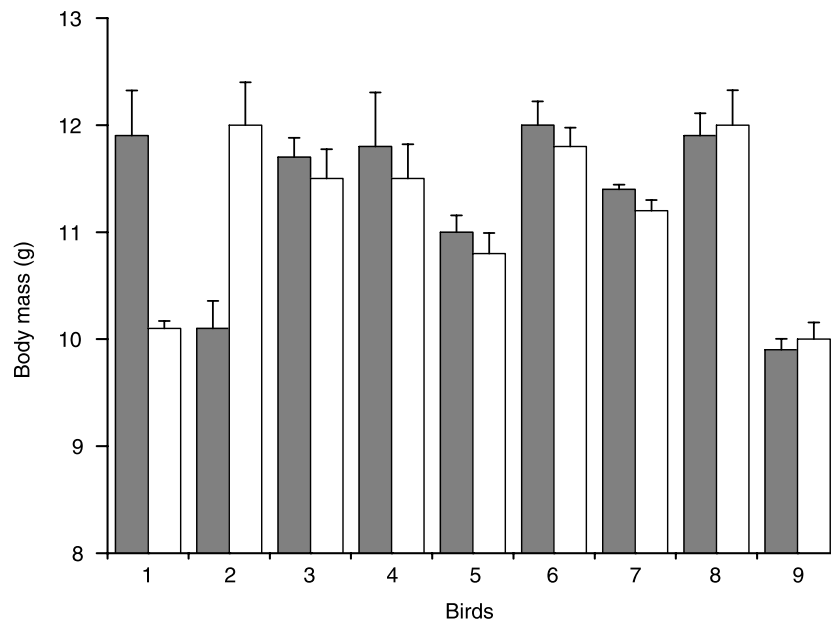


Figure 1. Mean body mass of individual birds as dominants and as subordinates. Dark bars show the birds when they appeared as dominants and white bars when they appeared as subordinates. Error bars are 95% confidence intervals. (No significant weight difference. $P = 0.47$, $n = 9$, paired t -test, two-tailed.)

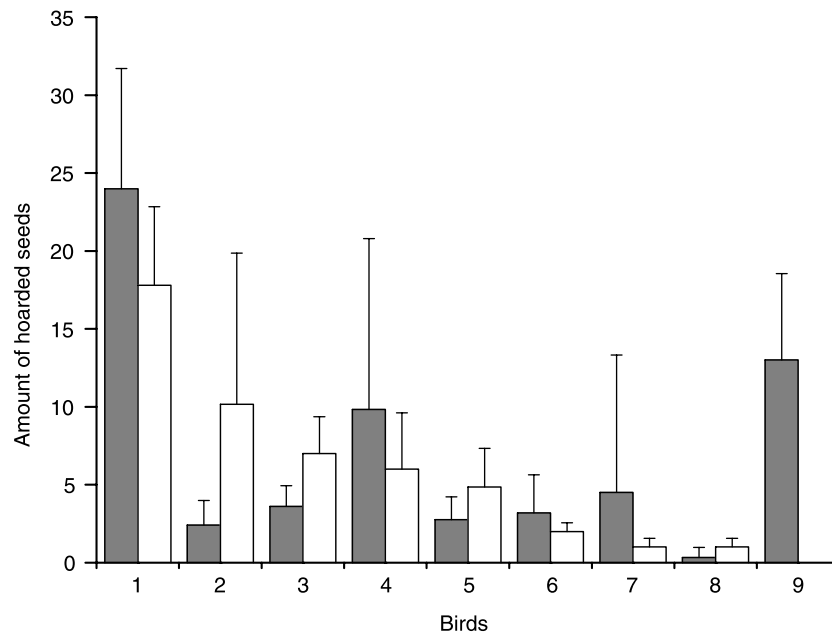


Figure 2. The mean number of seeds individual birds cached as dominant and as subordinate. Dark bars show birds as dominants and white bars as subordinates. Error bars are 95% confidence intervals. (No significant difference in the amount of food hoarding. $P = 0.78$, $n = 9$, paired t -test, two-tailed.)

& Ekman 1995, Brodin *et al.* 2001) may be wrong. Empirical evidence from the field suggests otherwise (Ekman & Lilliendahl 1993, Koivula *et al.* 1995; Lahti & Rytönen 1996, Lahti *et al.* 1998).

Secondly, the birds may not have evaluated their 'rank-role' in the same way as in a natural winter flock. An aviary is an artificial environment and birds may see it as something temporary and thus behave

in an unexpected way. This objection, however, goes for all aviary studies. Since the dominance ranks in the dyads were firmly established in the present study, any effect of rank on body fat reserves or hoarding should be detectable if they exist.

Thirdly, the cue for rank-dependent differences in foraging and fat acquisition strategies may not be dominance rank *per se*. When foraging in the wild, subordinate birds experience more variation in food availability than dominants. Hence the food availability experienced rather than the birds' perceived rank may be the mechanism that causes subordinate individuals to carry larger energy reserves. Such differences in food availability are difficult to assess, and we did not try to mimic them in our experiment.

Could there still be an effect?

There are also other possible explanations for our failure to find an effect, but we believe that we have controlled for these. Body fat status will affect the motivation to hoard, and the size of stored supplies will affect the urge to store. All birds had the same, *ad libitum* access to food, except for 1 h before the experiment. Thus all birds should have experienced the same food availability and could probably maintain their desired level of fat. This is also supported by the fact that most birds maintained the same level of fat throughout the experiment, and no bird had any stored supplies during the experiment.

Fat levels should increase through the day, prior to the overnight fast (e.g. Haftorn 1989, Lehtikoinen 1987), but may also vary between days. We only used midday body mass and found no systematic changes between days. This makes it probable that neither hoarding intensities nor decisions of fat acquisition were biased in any way by temporal fluctuations in the level of fat reserves. Temperature fluctuation between days could be a source of error, but since temperature fluctuations affected both dominants and subordinates equally during the experiments we think this unlikely to affect our results.

In nature subordinates avoid adverse interference by storing further from a feeder than dominants do (Lahti *et al.* 1998). This is not possible in an aviary and it is possible that subordinates stored less than they would have done in the field. However, 1 h is sufficient to give the subordinate birds many opportunities to take seeds from the tray.

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