

# Dominance, competition, and energetic reserves in the European starling, *Sturnus vulgaris*

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We investigated the relationships between social dominance, competition for food, and strategies of body mass and fat regulation in the European starling (*Sturnus vulgaris*). In birds housed in groups of three, subordinate birds stored more fat than dominants. A removal experiment established a causal link between social dominance and fat reserves; in groups that had the dominant individual removed, the remaining birds reduced body mass and fat, relative to control groups that had the subordinate removed. In a second experiment, we investigated the influences of degree of competition for food and dominance on body mass and fat reserves. Birds under high competition increased fat reserves and tended to have higher body mass than birds under low competition. The increase in fat reserves was higher in the subdominants than in the dominants. These results are consistent with hypotheses concerning dominance-dependent access to food; subordinate birds, or birds under increased competition, may store more fat as an insurance against periods when food cannot be obtained. However, relations between dominance, body mass, and fat reserves may also arise through other proximate factors relating to dominance-dependent costs and benefits of fat storage, such as predation risk and energetic expenditure. *Key words:* body mass, competition, dominance, European starling, fat reserves, lipids, regulation, *Sturnus vulgaris*. [*Behav Ecol* 6:343–348 (1995)]

Patterns of spatial and temporal variation in avian body mass and fat stores support the hypothesis that birds strategically regulate the size of their energetic reserves according to the relative costs and benefits of fattening (e.g., Lima, 1986; McNamara and Houston, 1987, 1990; Witter and Cuthill, 1993). The primary benefit of storing fat is that it provides an energetic reserve for periods when sufficient food cannot be obtained from the environment (see Blem, 1990). Such circumstances may arise predictably, for example during the night or a long migratory flight, or unpredictably, for example due to inclement weather, the intervention of other birds interrupting feeding, or simply due to the stochastic nature of foraging success. Fattening may also entail costs, for example due to increased energetic expenditure or increased risk of predation (see Witter and Cuthill, 1993). Theoretical analyses (e.g., Houston and McNamara, 1993; Lima, 1986; McNamara and Houston, 1987, 1990) predict that as the benefits of fattening increase, for example due to a deterioration in the energetic environment, birds should store higher levels of fat. Similarly, as the costs of fattening increase, such as an increased risk of predation, birds should store lower levels of fat. Such predictions are supported by several recent studies (e.g., Bednekoff, 1992; Ekman and Hake, 1990; Ekman and Lilliendahl, 1993; Rogers, 1987; Rogers and Smith, 1993; Rogers et al., 1993; Witter et al., 1994; Witter et al., in press).

The relationship between social dominance and fat reserves has been widely investigated. Most often dominants are found to store significantly more fat than subdominants (e.g., Baker and Fox, 1978; Fretwell, 1969; Millikan et al., 1985; Piper and Wiley, 1990; Wiedenmann and Rabenold, 1987). This relationship is often explained by the hypothesis that dominants obtain more or better food because they are able to displace subdominants from favorable feeding sites (e.g., Caraco, 1979; De Laet, 1985; Enoksson, 1988; Ficken et al., 1990; Piper and

Wiley, 1990). Since theoretical analyses predict that a decrease in mean energetic gain or predictability of food supply should result in increased energetic reserves (Lima, 1986; McNamara and Houston, 1990; see also Ekman and Lilliendahl, 1993), the food-access hypothesis must implicitly assume that subdominants' access to food is so restricted that it directly constrains the size of their energetic reserve. Less often considered is that subdominants may have lower optimal reserve sizes, rather than being constrained in the size of reserves, for example because the unit cost of storing fat is greater for subdominants (Witter and Cuthill, 1993). However, other relationships have also been reported between dominance and fat reserves. For example, Nolan and Ketterson (1983) found no relationship in dark-eyed juncos (*Junco hyemalis*), while Gosler (1987) and Ekman and Lilliendahl (1993) found subdominants stored more fat than dominants in great tits (*Parus major*) and willow tits (*Parus montanus*). The latter findings were interpreted as a strategic response by the subdominants to a less predictable food supply. That is, because subdominants were more likely to be interrupted during foraging, they stored higher levels of fat as an insurance against the periods without food.

Most of the evidence that dominance influences fat reserves is observational; few studies have attempted to show that the relationship is causal by manipulating either dominance or the social environment. An exception is Ekman and Lilliendahl's (1993) investigation of the relationship between energetic reserves and dominance in the willow tit. Ekman and Lilliendahl (1993) found that subordinate birds stored significantly more fat than dominants and that when the dominants were removed the subordinate birds reduced fat stores compared with subdominants in unmanipulated controls. This experiment is important to identify whether differences in the size of energetic reserves between dominance classes are causally related to the social environment. However, there is an important confounding factor in the manipulation: the control treatments were unmanipulated, so differences in change in group size exist between treatments. This may influence, for example, degree of competition for

food, which may affect the size of energetic reserve independently or in addition to changes in the social environment. In this article, we directly address these possibilities by examining the relationships between social dominance, competition for food, body mass, and fat reserves in the European starling (*Sturnus vulgaris*). In the first experiment, we examine whether dominance is causally related to fat reserves by manipulating the social environment. Our manipulation is based on Ekman and Lilliendahl's (1993) study in that half of the experimental groups have the dominant bird removed; however, our control groups have the most subdominant bird removed. In this way, we manipulate the social environment of the remaining birds without introducing the confounding factor of number of birds present in each group. In the second experiment, we investigate whether degree of competition for food influences fat reserves and whether this effect differs according to dominance class by manipulating the number of birds that can simultaneously access feeders.

## METHODS

### Experiment 1

Experiment 1 was performed on 36 wild-caught adult female starlings. We randomly allocated birds to 12 groups, each containing three birds, and housed all groups in identical cages, measuring  $1.0 \times 0.3 \times 0.3$  m, in visual isolation, maintained at a constant temperature of 20°C, under an 8L:16D photoperiod. Food (turkey starter crumbs) was available ad libitum from two food hoppers placed at the center of the cage front. Water was also available ad libitum from two dispensers placed at opposite ends of the cage. After 1 week in these conditions, initial measurements were taken. We measured body mass (to 0.1 g) on an electronic balance and a score of subcutaneous fat (0–5) was taken according to the criteria of Helms and Drury (1960). These and all subsequent measures of body mass and fat were taken within 1 h of dawn to control for any diurnal variation in these variables.

The following day, we took scores of dominance. All birds were food deprived for 2 h. Immediately after the return of the food hopper, all dominance interactions, in which one bird clearly displaced another, were recorded for 15 min. This procedure allowed birds in each group to be assigned a dominance rank of 1 (most dominant) to 3 (least dominant). Two days after these observations were taken, half of the groups had the least dominant bird removed; the remaining groups had the most dominant bird removed. We arranged removal of birds so that treatment-group cages alternated. Thus, this manipulation alters the dominance composition of the groups without confounding effects of the number of conspecifics present. Following these changes, body mass and fat score were recorded at intervals of 2 or 3 days, with each set of measurements beginning at dawn, for approximately 3 weeks.

### Experiment 2

We performed the experiment on 48 wild-caught juvenile starlings. All individuals were allocated randomly to 12 groups of four birds, housed in cages measuring  $0.5 \times 0.5 \times 0.3$  m, in visual isolation, maintained at a temperature of 20°C. In this experiment, birds were maintained under simulated natural photoperiod (starting at 18L:6D, reduced in 30 min steps). After 1 week, we recorded initial measures of body mass and fat score, as described above. These groups were then divided into two treatments: high competition and low competition. In both cases, food and water were available ad libitum. However, the low competition groups could obtain food from two feeders, a single small feeder that could only be accessed by

one bird at a time and a long open feeder, which all birds could access simultaneously. The high competition groups could obtain food only from a single small feeder. The long open feeding tray was present in the high competition cages, but it did not contain food. Thus, this manipulation alters degree of competition for food without simultaneously changing the amount of open or perching space available between treatments. We recorded body mass and fat score again after 3 weeks. Dominance observations, as described for experiment 1, were taken in the first week of the treatment, allowing each bird in each cage to be assigned dominance ranks of 1 (most dominant) to 4 (least dominant).

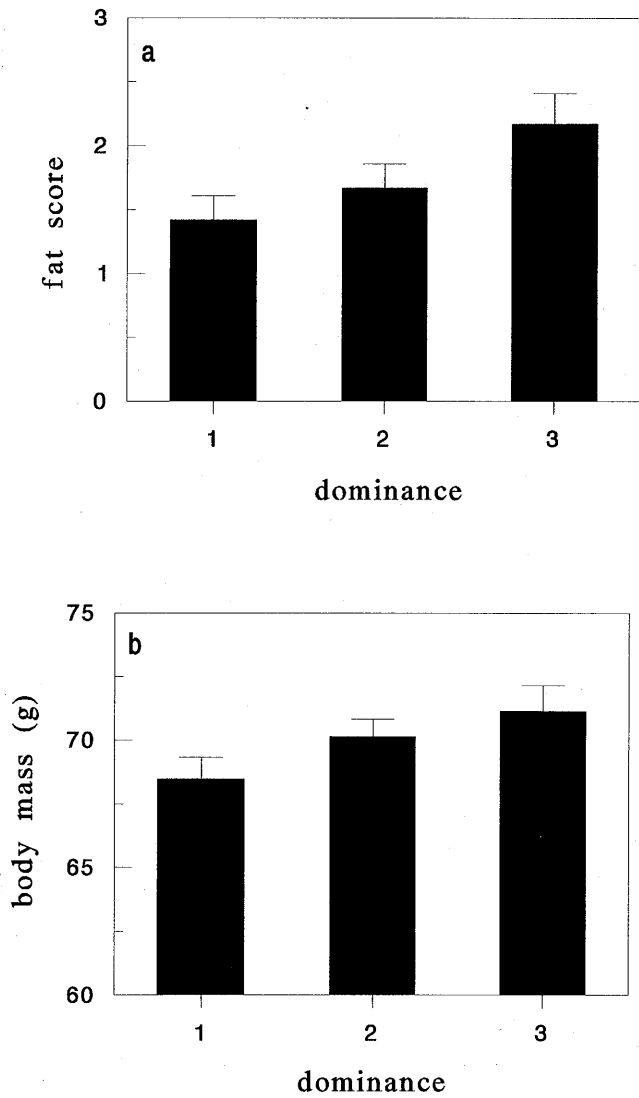
### Statistical analyses

To avoid pseudoreplication (Hurlbert, 1984), we treat each cage, rather than each individual, as the independent experimental units (cf. Witter et al., 1994); individuals within each cage are treated as within-subject repeated measures. We analyzed changes in body mass by univariate mixed-model repeated-measures analysis of variance (see Hand and Taylor, 1987), using MANOVA on SPSS (SPSS, 1988). Fat scores have been analyzed by Friedman's analysis of variance (Siegel and Castellan, 1988) or, where the assumptions of parametric analyses were fulfilled, by repeated-measures ANOVA. We have transformed data where appropriate to meet the assumptions of the tests employed. Normality of the data or residuals was investigated by normal probability plots. Results are shown as mean ( $\pm$  SE), and two-tailed tests of significance have been used throughout.

## RESULTS

### Experiment 1

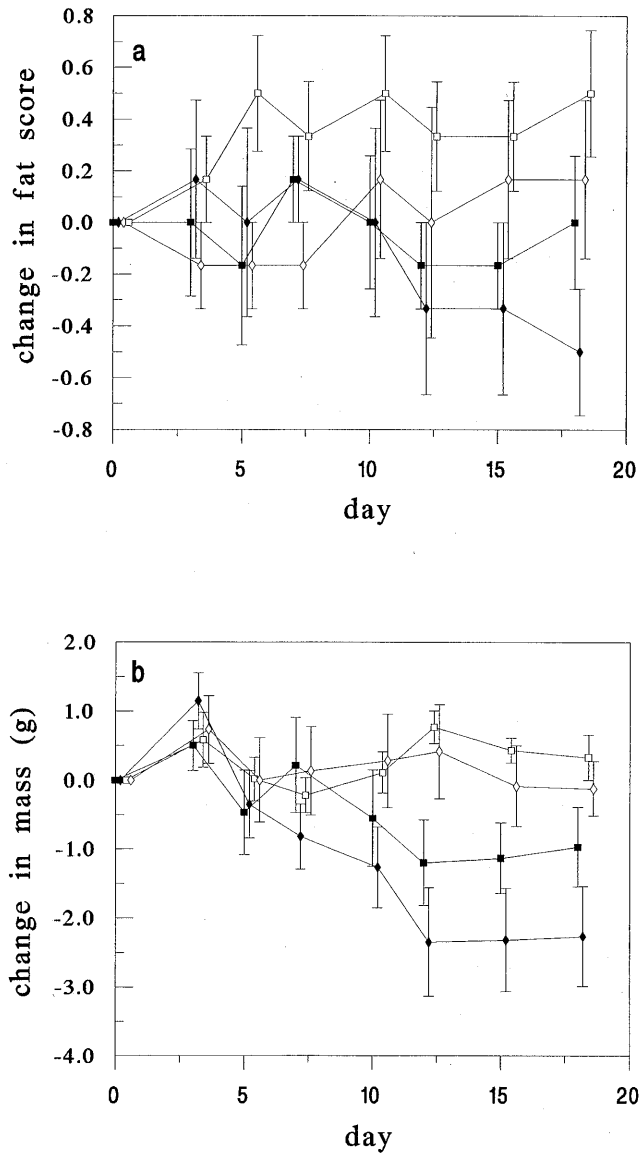
At the start of experiment 1, dominants stored significantly less fat than subdominants (Friedman's ANOVA,  $S_2 = 8.43$ ,  $p = .015$ ; Figure 1a). Dominants also showed a trend toward lower mass, although this difference was not quite significant ( $F_{2,22} = 3.05$ ,  $p = .065$ ; Figure 1b). Following the manipulation of social composition of the groups, there was a significant difference in change in body mass between the two treatments (significant Group  $\times$  Day interaction; Table 1; Figure 2b). In groups where the dominants were removed, the remaining birds lost mass, whereas in the groups where the subdominants were removed, the remaining birds exhibited no overall change in mass. Changes in mass over the experiment differed according to dominance rank per se (significant Dominance  $\times$  Day interaction), with the subdominant birds losing more mass on average; this change did not differ according to treatment group (nonsignificant Group  $\times$  Dominance  $\times$  Day interaction). The mass of dominants also differed according to treatment (significant Group  $\times$  Dominance interaction). This is simply a reflection of the manipulation: dominance ranks 1 and 2 in this stage of the experiment were, at the start of the experiment, ranks 1 and 2 in the groups with the subdominant removed and ranks 2 and 3 in the groups with the dominant removed. Changes in fat score showed a similar pattern (Table 1; Figure 2a). Groups with dominants removed lost fat over the course of the experiment compared with groups that had subdominants removed (significant Group  $\times$  Day interaction). As with body mass, changes in fat also differed according to dominance status (significant Dominance  $\times$  Day interaction). These results indicate that the initial relationship between dominance and fat was causally related to the birds' social environment; subdominants, which initially maintained higher levels of reserves than dominants, lost mass and fat when the dominants were removed.



**Figure 1**  
Mean (+SE) (a) fat score and (b) body mass versus dominance rank at the start of experiment 1. Rank 1 is the most dominant and rank 3 is the least dominant bird from the 12 groups of three birds.

**Table 1**  
ANOVAs on body mass and fat score from experiment 1

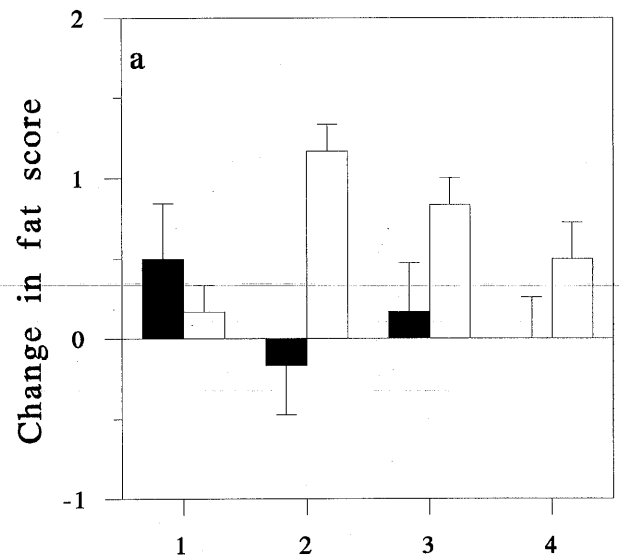
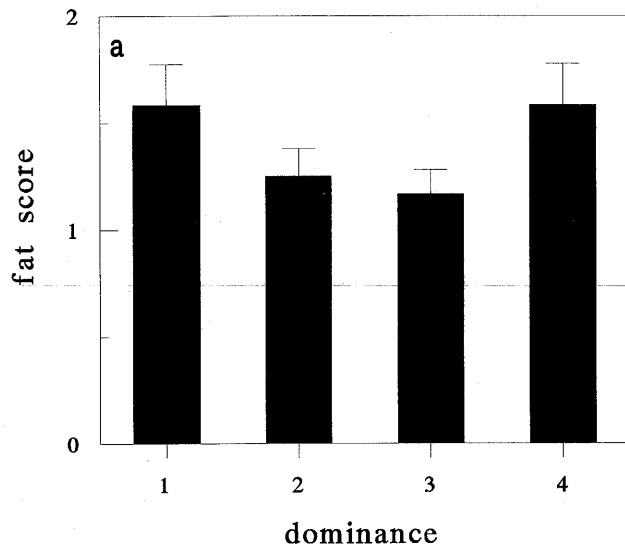
Variable	Factor	df	F	P
Body mass	Treatment	1,10	3.00	.114
	Day	7,70	8.89	<.001
	Dominance	1,10	0.14	.717
	Treatment*Day	7,70	8.57	<.001
	Treatment*Dominance	1,10	9.40	.012
	Day*Dominance	7,70	2.35	.032
	Treatment*Day*Dominance	7,70	1.72	.118
Fat score	Treatment	1,10	0.22	.648
	Day	7,70	0.70	.670
	Dominance	1,10	1.06	.327
	Treatment*Day	7,70	2.64	.018
	Treatment*Dominance	1,10	0.29	.601
	Day*Dominance	7,70	2.46	.026
	Treatment*Day*Dominance	7,70	0.63	.726



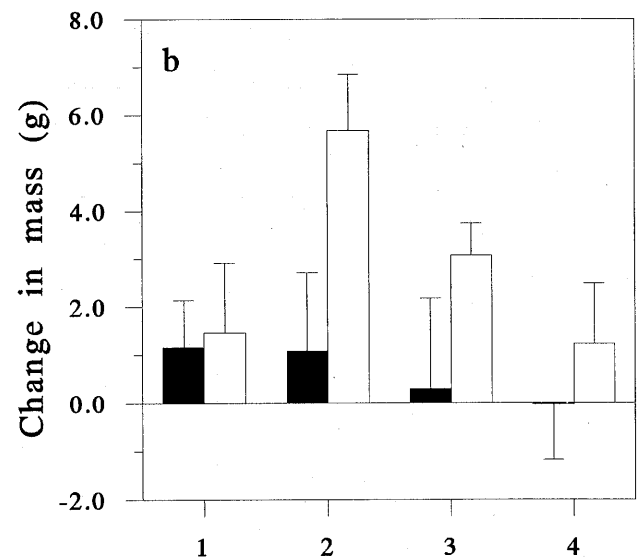
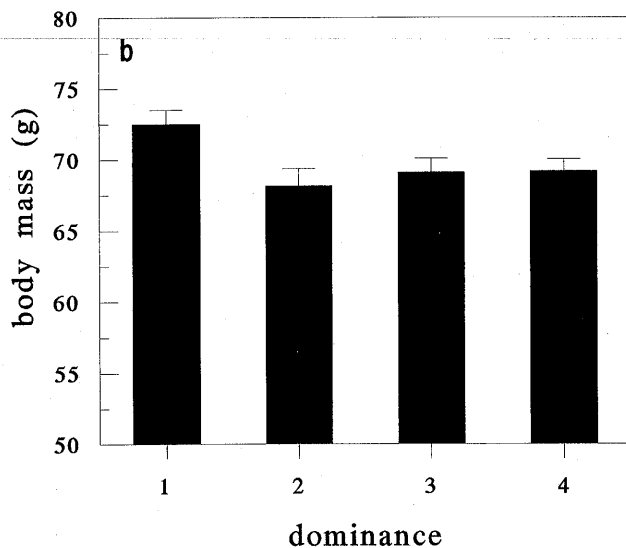
**Figure 2**  
Mean ( $\pm$ SE) change in (a) fat score and (b) body mass following the manipulations in experiment 1. Closed symbols are the groups with the dominant birds removed and open symbols are the groups with the subdominant bird removed. Squares show the remaining dominants, and diamonds show the remaining subdominants.

**Experiment 2**

The initial relationships between dominance, fat reserves, and body mass from experiment 2 are shown in Figure 3. There were significant differences in fat reserves between dominance ranks ( $F_{3,11} = 6.18, p = .010$ ), with a similar trend for body mass ( $F_{3,11} = 3.20, p = .066$ ). However, the pattern of relationship is different in this experiment compared with experiment 1. In this case, there is a significant U-shaped relation between dominance and fat reserves (Quadratic contrast,  $t_{11} = 2.944, p = .007$ ). Fat reserves changed according to the manipulation of competition for food (Figure 4a); birds under higher competition responded by increasing fat reserves ( $F_{1,11} = 11.17, p = .007$ ). However, the response to competition differed according to dominance rank (Group  $\times$  Dominance interaction,  $F_{3,11} = 4.47, p = .027$ ). Subdominant birds responded to the manipulation by increasing fat reserves to a



Dominance



Dominance

**Figure 3**

Mean (+SE) (a) fat score and (b) body mass versus dominance rank at the start of experiment 2. Rank 1 is the most dominant and rank 4 the least dominant birds from the 12 groups of four birds.

greater extent than the dominants (Figure 4a). Unlike changes in fat, change in body mass did not differ significantly by treatment or dominance rank, although the trend is similar to fat score (Group,  $F_{1,11} = 3.46$ ,  $p = .070$ ; Dominance,  $F_{3,11} = 1.54$ ,  $p = .219$ ; Group  $\times$  Dominance,  $F_{3,11} = 2.00$ ,  $p = .130$ ; Figure 4b).

## DISCUSSION

At the start of the first experiment, subordinate birds had larger fat reserves and tended to have higher body mass than dominants. This pattern is similar to that observed in willow tits (Ekman and Lillendahl, 1993) and great tits (Gosler, 1987). The manipulation established a causal link between dominance status, body mass, and fat reserves; when the dominant birds were removed, subdominants lost mass and fat compared with the control groups with subdominants re-

**Figure 4**

Mean (+SE) change in (a) fat score and (b) body mass, during the three weeks following the start of the manipulation of competition for food in experiment 2, versus dominance rank. Rank 1 is the most dominant and rank 4 the least dominant. Open bars are the high competition group, and solid bars are the low competition group.

moved. This indicates that the presence of the dominant was responsible for the higher body mass and fat reserves of the subordinate birds. Unlike the study of Ekman and Lillendahl (1993), our experiment ruled out an influence of number of birds present in each treatment group, which might influence degree of competition, because the number of birds in each treatment was the same following the manipulation. Experiment 2 demonstrated that degree of competition for food influenced fat reserves; birds under higher competition

increased fat reserves in comparison with groups under lower competition.

The mechanism through which dominance influences fat reserves is usually proposed to be differential access to food (see Witter and Cuthill, 1993). Where dominants are found to store more fat, this is often attributed to their access to more or better quality food (e.g., Caraco, 1979; De Laet, 1985; Enoksson, 1988; Ficken et al., 1990; Piper and Wiley, 1990). This hypothesis implicitly assumes that subdominants' fat reserves are constrained by food availability (Witter and Cuthill, 1993). Subdominants having been found to have higher fat reserves than dominants has been attributed to a strategic response to a reduced rate of gain or reduced gain predictability, with subdominants maintaining higher reserves as an insurance against times when food cannot be obtained (Ekman and Lilliendahl, 1993). Such hypotheses are not necessarily in contradiction. It is feasible that under low levels of interaction subdominants are able to increase their fat reserves strategically, whereas under high levels of interaction subdominants are constrained by access to food. However, the finding that subdominants have lower levels of reserves does not constitute evidence of food limitation (cf. King and Murphy, 1985). Without additional evidence, such results could be equally well explained by subdominants having lower optimal reserves (Witter and Cuthill, 1993; see below).

Our results are consistent with a dominance-dependent food-access hypothesis. In experiment 1, subdominant birds may have maintained higher fat reserves because they were more likely to be interrupted while feeding; thus, the benefits of fattening would be higher to a subdominant, all else being equal (McNamara and Houston, 1990). When the dominant bird was removed, the likelihood of effective interruptions decreased and fat reserves decreased in association. Similarly, increased competition in experiment 2 resulted in increased fat reserves; this increase was greatest in the subdominant birds. It is likely that increased competition would have a larger effect on subdominants because of their low competitive status. Thus, they may have compensated for the increased interruption rate by increasing the size of fat reserve. Evidently, the increased interruption rate did not constrain food intake. Instead, the birds strategically increased food intake in response to the manipulation. Analogously, Witter and Swaddle (1994) showed that the relationship between the development of fluctuation asymmetries in primary feathers and dominance status varied according to the degree of competition for food; subdominants exhibited larger increases in asymmetry than dominants when competition for food increased. Interruptions while foraging may influence, for example, predictability of food supply or mean time available to feed. Experimental manipulations of these aspects of food availability have been shown to result in increased body mass and fat reserves in a range of avian species (e.g., Bednekoff, 1992; Ekman and Hake, 1990; Hurlly, 1992; Witter et al., in press).

Witter and Cuthill (1993) proposed that the widely reported positive relation between dominance and fat reserves may be accounted for by dominance-dependent differential costs of fattening. If the marginal cost of fattening is greater to a subdominant than to a dominant then, all else being equal, dominants will have higher optimal reserves. This may arise, for example, because dominants are under a lower predation risk than subdominants (e.g., De Laet, 1985; Hegner, 1985; Hogstad, 1988; Lima et al., 1987). Additionally, however, the benefits of fattening also depend on dominance. Differential access to food (e.g., Caraco, 1979; De Laet, 1985; Enoksson, 1988; Ficken et al., 1990; Piper and Wiley, 1990) or differential energetic expenditure, for example because dominants have access to better roost sites (e.g., Summers et al., 1986; Swing-

land, 1987; Weatherhead and Hoysack, 1984), may increase the benefits of fattening for subdominants. However, if dominants have higher metabolic rates than subdominants (Hogstad, 1987; Røskaft et al., 1986), the benefits of fattening may be higher for a dominant. Such cost/benefit reasoning suggests two distinct circumstances of competition under which dominants might have higher energetic reserves than subdominants. With dominance-dependent costs of fattening, dominants should store higher reserves under low levels of competition because differential benefits of fattening may be slight. Under severe levels of competition, subdominants' energetic reserves will be constrained by food availability; under such circumstances, dominants may also store more fat. Between these extremes of competition, a continuum of possible outcomes is feasible. A priori, there is no theoretical justification for assuming that the relationship between dominance and energetic reserves should always be monotonic (see Witter and Cuthill, 1993). It is thus of interest that there was a significant U-shaped relation between fat reserves and dominance at the start of experiment 2. Such a relation may arise, for example, as a result of the costs and benefits of fattening decreasing at differential rates with increasing dominance. Since a continuum of possible relations between dominance and energetic reserves is feasible, the relation between dominance and fat reserves alone should not be used to make inferences about degree of competition, or, more generally, about the proximate factors through which the relationship arises. This is considered in more detail below.

Although our experiments demonstrate causal relationships between dominance, competition, fat reserves, and mass, such experiments do not allow us to make direct inferences about the mechanism through which these effects act. This point is rarely acknowledged in the literature (Witter and Swaddle, 1994). Thus, while our results are consistent with hypotheses relating to dominance-dependent access to food, differences among dominance classes extend beyond differential access to food. For example, dominance may be related to between-individual variation in metabolic rate (e.g., Hogstad, 1987; Røskaft et al., 1986), endocrine physiology (e.g., Silverin et al., 1984), anti-predatory behavior (e.g., De Laet, 1985; Hegner, 1985; Hogstad, 1988) and habitat selection (e.g., Ekman and Askenmo, 1984; Fretwell, 1969). Any of these factors instead of, or in addition to, differential access to food may influence fat reserves (see Houston and McNamara, 1993; Lima, 1986; McNamara and Houston, 1987, 1990). Additionally, dominance of an individual and the dominance structure of groups may change when the context of interactions change (Lee, 1983; see also Witter and Swaddle, 1994). Thus, to decide the mechanism through which dominance influences fat reserves, it is necessary to disentangle experimentally changes in aggressive interactions, dominance status, and differential access to food.

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## REFERENCES

- Baker MC, Fox SF, 1978. Dominance, survival and enzyme polymorphism in dark-eyed juncos, *Junco hyemalis*. *Evolution* 32:697-711.
- Bednekoff PA, 1992. Foraging and fat reserves in great tits in a variable environment (DPhil thesis). Oxford: University of Oxford.
- Blem CR, 1990. Avian energy storage. *Curr Ornithol* 7:59-113.

- Caraco T, 1979. Time budgeting and group size: a test of a theory. *Ecology* 60:618–627.
- De Laet JF, 1985. Dominance and anti-predator behaviour of great tits, *Parus major*: a field study. *Ibis* 127:372–377.
- Ekman JB, Askenmo C, 1984. Social rank and habitat use in willow tit groups. *Anim Behav* 32:508–514.
- Ekman JB, Hake MK, 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 JB, Lilliendahl K, 1993. Using priority to food access: fattening strategies in dominance-structured willow tit (*Parus montanus*) flocks. *Behav Ecol* 4:232–238.
- Enoksson B, 1988. Age and sex differences in dominance and foraging behaviour of nuthatches (*Sitta europaea*). *Anim Behav* 36:231–238.
- Ficken M, Weise C, Popp J, 1990. Dominance rank and resource access in winter flocks of black-capped chickadees. *Wilson Bull* 102:623–633.
- Fretwell S, 1969. Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*). *Bird Band* 40:1–83.
- Gosler A, 1987. Aspects of bill morphology in relation to ecology in the great tit, *Parus major* (DPhil thesis). Oxford: University of Oxford.
- Hand DJ, Taylor CC, 1987. Multivariate analysis of variance and repeated-measures: a practical approach for behavioural scientists. London: Chapman Hall.
- Hegner RE, 1985. Dominance and anti-predator behaviour in blue tits (*Parus caeruleus*). *Anim Behav* 33:762–768.
- Helms CW, Drury WH, 1960. Winter and migratory weight and fat: field studies on some North American buntings. *Bird Band* 31:1–40.
- Hogstad O, 1987. It is expensive to be dominant. *Auk* 104:333–336.
- Hogstad O, 1988. Social rank and anti-predatory behaviour of willow tits, *Parus montanus*, in winter flocks. *Ibis* 130:45–56.
- Houston AI, McNamara JM, 1993. A theoretical investigation of fat reserves and mortality levels in small birds in winter. *Ornis Scand* 24:205–219.
- Hurlbert SH, 1984. Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54:187–211.
- Hurly AT, 1992. Energetic reserves of marsh tits (*Parus palustris*): food and fat storage in response to variable food supply. *Behav Ecol* 3:181–188.
- King JR, Murphy ME, 1985. Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? *Am Zool* 25:955–964.
- Lee PC, 1983. Context specific unpredictability in dominance interactions. In: Primate social relationships (Hinde RA, ed). Oxford: Blackwell; 35–44.
- Lima SL, 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67:377–385.
- Lima SL, Wiebe KL, Dill LM, 1987. Protective cover and the use of space by finches: is closer better? *Oikos* 50:225–230.
- McNamara JM, Houston AI, 1987. Starvation and predation as factors limiting population size. *Ecology* 68:1515–1519.
- McNamara JM, Houston AI, 1990. The value of fat reserves and the trade-off between starvation and predation. *Acta Biotheor* 38:37–61.
- Millikan GC, Gaddis P, Pulliam HR, 1985. Interspecific dominance and the foraging behaviour of juncos. *Anim Behav* 33:428–435.
- Nolan V, Ketterson ED, 1983. An analysis of body mass, wing length and visible fat deposits of dark-eyed juncos wintering at different latitudes. *Wilson Bull* 95:603–620.
- Piper WH, Wiley RH, 1990. The relationship between social dominance, subcutaneous fat, and annual survival in wintering white-throated sparrows (*Zonotrichia albicollis*). *Behav Ecol Sociobiol* 26:201–208.
- Rogers CM, 1987. Predation risk and fasting capacity: do winter birds maintain optimal body mass? *Ecology* 68:1051–1061.
- Rogers CM, Nolan V, Ketterson ED, 1993. Geographic variation in winter fat of dark-eyed juncos: displacement to a common environment. *Ecology* 74:1183–1190.
- Rogers CM, Smith JNM, 1993. Life-history theory in the nonbreeding period: trade-offs in avian fat reserves. *Ecology* 74:419–426.
- Røskft E, Jarvi T, Bakken M, Bech C, Reinertsen RE, 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.
- Siegel S, Castellan NJ, 1988. Nonparametric statistics for the behavioral sciences, 2nd ed. Singapore: McGraw-Hill.
- Silverin B, Viebke PA, 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.
- SPSS, 1988. SPSSx user's guide, 3rd ed. Chicago: SPSS.
- Summers RW, Westlake GE, Feare CJ, 1986. Differences in the ages, sexes and physical condition of starlings in the centre and periphery of roosts. *Ibis* 129:96–102.
- Swingland IR, 1987. The social and spatial organization of communal roosting in rooks (*Corvus frugilegus*). *J Zool Lond* 182:509–528.
- Weatherhead PJ, Hoysack DJ, 1984. Dominance structuring of a re-winged blackbird roost. *Auk* 101:551–555.
- Wiedenmann RN, Rabenold KN, 1987. The effects of social dominance between two subspecies of dark-eyed juncos, *Junco hyemalis*. *Anim Behav* 35:856–864.
- Witter MS, Cuthill IC, 1993. The ecological costs of avian fat storage. *Phil Trans R Soc Lond B* 340:73–90.
- Witter MS, Cuthill IC, Bonser RHC, 1994. Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Anim Behav* 48:201–222.
- Witter MS, Swaddle JP, 1994. Fluctuating asymmetries, competition and dominance. *Proc R Soc Lond B* 256:299–303.
- Witter MS, Swaddle JP, Cuthill IC, in press. Periodic food availability and strategic regulation of body mass in the European starling, *Sturnus vulgaris*. *Funct Ecol*.